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The Autecology of
Hudsonia tomentosa in Northern Alberta

by

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

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Date Oct. 15, 1984

ABSTRACT

The autecology of Hudsonia tomentosa Nutt., was studied in the Pinus banksiana/Cladina mitis lichen woodlands of northeastern Alberta. Hudsonia was found throughout the study area on stabilized and unstabilized aeolian landforms and was determined to be the major pioneer species of disturbed open sand sites such as roadsides, burn sites, blowouts and large dune systems (e.g. the Maybelle River Dune System). Revegetation of these sites always occurred after Hudsonia dominance.

Hudsonia is a dwarf semi-evergreen heath-like shrub which disperses into open sand either by outward expansion of a clone-forming habit or by wind aided dispersal of seed containing fruit. Seeds are long lasting and tend to collect in large numbers in slight depressions.

Hudsonia's role in changing vegetation patterns was related to its capacity for dune building thereby altering local microclimates and to its role in providing substrate for lichen attachment. Decline in Hudsonia dominance coincided with lichenization. The xeric nature of the study area, the frequency of disturbance, the presence of ridge top blowouts and large open sand dune systems and the high carbon allocation to reproduction ensure local prominance of Hudsonia.

In this thesis several autecological characteristics of Hudsonia are described which relate to its ability to colonize and thrive on open, xeric, nutrient poor sands.

In terms of the xeric nature of these sites, Hudsonia was able to control its water relations and followed seasonal and diurnal patterns similar to many temperate zone broadleaf evergreen shrubs. Mid-day plateaus in xylem tension occur at 1.3 to 1.5 MPa. A combination of small reductions in leaf and stem conductance, combined with a high frequency of mid-day cloud build-up and precipitation events, ensure that Hudsonia does not normally develop severe moisture stress. Hudsonia exhibits preferential maintenance of plant water status within a plant which ensures the longevity of at least some plant parts during periods of severe moisture stress.

This study has determined that Hudsonia possesses a free-living nitrogen fixing microbial association. Hudsonia was the only vascular plant for which nitrogen fixation was detected. Although rates, as measured by acetylene reduction, were low (maximum rate of 1 nmole (C_2H_4.g soil^{-1}.hr^{-1}), they are probably significant in these nutrient poor sands. Seasonal variation in fixation was largely explained by a 30% soil water content optima and a 28-33°C temperature optima. Blue green algae (Oscillatoria, Lyngbya, Nostacaceae-type and Microcystis were isolated) appear to be responsible for the nitrogen fixation detected in the buried phyllosphere and rhizosphere of Hudsonia. This free-living nitrogen-fixing blue green algal association is unique to Hudsonia and warrants further investigation.

Hudsonia was able to withstand moderate levels of sand movements (depositional and deflation). Not only was Hudsonia able to withstand sand deposition, its net annual production and mean length of vegetative growth were stimulated by deposition. This ability may be the single most important factor determining why *Hudsonia* and not other native species, e.g. *Empetrum nigrum*, are colonizing these open sands. *Hudsonia* exhibited a flexibility in growth and carbon allocation patterns in respose to a varied pattern of sand movement. As much as 95% allocation to vegetative growth and 87% allocation to reproductive growth were found.

The findings were summarized in a word model depicting the fate of *Hudsonia* in the *Pinus*-lichen woodland. The importance of *Hudsonia* in relation to revegetation of Alberta's Oil Sands was noted.

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INTRODUCTION

The development of Alberta's oil sands has generated a considerable amount of interest in the ecology of northeastern Alberta. Until this time, neither the climate, hydrology, nor the vegetation had been studied to any degree. One of the major concerns that developed was the long-term stabilization of disturbed Alberta oil sands. Large masses of sand (a byproduct of oil extraction) would have to be stabilized in order to avoid the development of large active sand dunes within the area. Several studies were initiated by industry and provincial agencies to determine the proper plant species and techniques required for revegetation. An important consideration, apparently overlooked, was the identification of which native species in the area were capable of colonizing and stabilizing large open sand areas. A preliminary field survey (in northeastern Alberta) by Drs. Bliss and Mayo to determine the species and their autecological character lead to the realization that *Hudsonia tomentosa* Nutt. was a major colonizer of open sands (Plate 1). Field observations indicated that exceptional growth of *Hudsonia* (Plate 2) took place in these xeric, nutrient poor sands. This thesis was undertaken in order to determine the autecological character of *Hudsonia* which allowed it to colonize, thrive and stabilize these areas. It was hoped that findings would provide important information regarding *Hudsonia*'s adaptation to water, nutrient and sand movement stresses which could assist in the selection of plant characteristics required for stabilization of worked oils sands.

Plate 1 Extent of Hudsonia colonization and stabilization at the Blowout study site.

COLOURED PICTURES
Images en couleur

Plate 2 Exceptional growth of a single Hudsonia plant. The 15 cm ruler is placed at a zone of adventious rooting from the base of last year growth. This site was at the base of a strongly depositional slope.

COLOURED PICTURES
Images en couleur

H. tomentosa is a dwarf semi-evergreen heath-like shrub, 0.5 to 2 dm high and 2 to 6 dm in diameter, forming closed mats or singly scattered. Leaves are alternate, closely appressed and covered by a heavy pubescence. Flowers are small, showy, short-lived and have five yellow petals and five sepals. The fruit is a one loculed capsule, few seeds with a persistent calyx (Moss, 1959). The seeds are noted for their 'copious' endosperm.

The genus Hudsonia has not received much scientific attention. The taxonomy has been particularly confused. Hall (1956) and Skog and Nickerson (1972) have recognized several subspecies and concluded that H. tomentosa Nutt. was a subspecies of H. ericoides L. Other subspecies of H. ericoides that were recognized in these studies include subsp. intermedia Peck., montana Nutt., ericoides and andersonii. Morse (1979), presents a convincing comprehensive review of the genus and recognizes three separate species: H. ericoides, H. montana and H. tomentosa. He suggests that a woody xerophytic Helianthemum was the phyletic ancestor of the genus. Also, that H. tomentosa represents the most xerophytic extension (H. montana -- H. ericoides -- H. tomentosa) within the genus. The following characteristics of H. tomentosa were noted as significant xerophytic variations between the three species; reduction in leaf size and pedicel length, increase in length of short shoot supporting flowers, increase in the density of pubescence, and a promptly deciduous fruit. Morse (1979) also concluded that the three species exhibit different site preferences even though a certain degree of overlap occurs. H. montana is limited to quartzite ledges in the Catawba Range, near Table Rock, Burke Co., NC. H. ericoides is not densely pubescent, leaves although appressed are essentially free and flowers are on slender naked pedicels 4 to 10 mm long. It is more shade tolerant than H. tomentosa and is more limited to inland sandy acidic pine barrens from Delaware to New Hampshire and Maine to Newfoundland. H. tomentosa, on the other hand, is important in coastal dunes (especially involved in the stabilization of barrier island dunes) as well as upland sand plains and sandstone outcrops. It occurs from southern Ontario northwest to Illinois, Minnesota and Saskatchewan, north to northern Alberta, and along the coast from Gaspé Penninsula through the Maritime Provinces and Maine to New Hampshire.

Morse (1979) reports an extension of H. tomentosa northward up to Great Slave Lake. He discusses four possible areas of mid-glacial occurrence which include extensive shore areas along the Atlantic coastline, the Driftless Area of southwestern Wisconsin on glacial outwash, unglaciated land of Alberta and a small isolated site at Panthere Knob, Virginia. Based on pollen evidence (Brubaker, 1975) from the ice border in Michigan and this northern extension of Hudsonia, Morse hypothesizes that Hudsonia was a major colonizer of glacial outwash, and spread into extensive sandy uplands. However, with time its range has diminished as sand deposits deflated or became more densely vegetated. He suggests that to a large extent its current range is restricted to sandy sites of intermittent or continued disturbance.

In this study only sites of H. tomentosa in northeastern Alberta were studied. Site (physical and synecological), autecological, ecophysiological characteristics are described in an attempt to better understand where, how and why Hudsonia is able to colonize and thrive on these open sand sites. In addition a free-living N_2 fixation-association with Hudsonia is described. Hudsonia at the study sites have characteristics similar to those described for H. tomentosa and have been identified as such (Morse-personal comm.).

STUDY SITE; PHYSICAL CHARACTERISTICS

INTRODUCTION

Two study sites were located in northeastern Alberta (Fig. 1). The 'Blowout' site (Plate 3) was situated on a small (0.03 km^2) terminal crest of a longitudinally oriented semi-stabilized dune (Twp 104, R7, W4). The 'Dune' site (Plate 4) was located at a large (16 km^2) active dune field (Sections 28 and 33, Twp 105, R6, W4), designated as the Maybelle River Dune System by Raup and Argus (1982). These sites were chosen due to the proximity of Richardson Fire Tower airstrip (Section 26, Twp 102, R7, W4) and of an Alberta Oil Sands Environmental Research Program (AOSERP) Research project (Project VE 6.1, see Bliss and Mayo, 1980).

The Land Region (mapping scale 1:1,000,000-1:3,000,000) surrounding the study sites has been defined as Boreal Forest (Rowe 1972). The climate is continental with long cold winters and cool short summers, or cold temperate (mean temperature for warmest month $>10°C$, mean temperature for coldest month $<-3°C$, and less than 4 months with mean temperature $>10°C$) according to the Koppen classification scheme. The mean annual length of growing season is 140-160 d (Rowe 1972). General atmospheric circulation is from west to east, with upper level air flow from WNW to ESE (Longley and Janz, 1978). The majority of the precipitation falls in the five summer months (May to September); the mean precipitation for this period is 200-250 mm (Northeast Alberta Regional Commission, 1978). The moisture regime is defined as dry sub-humid (Rowe 1972).

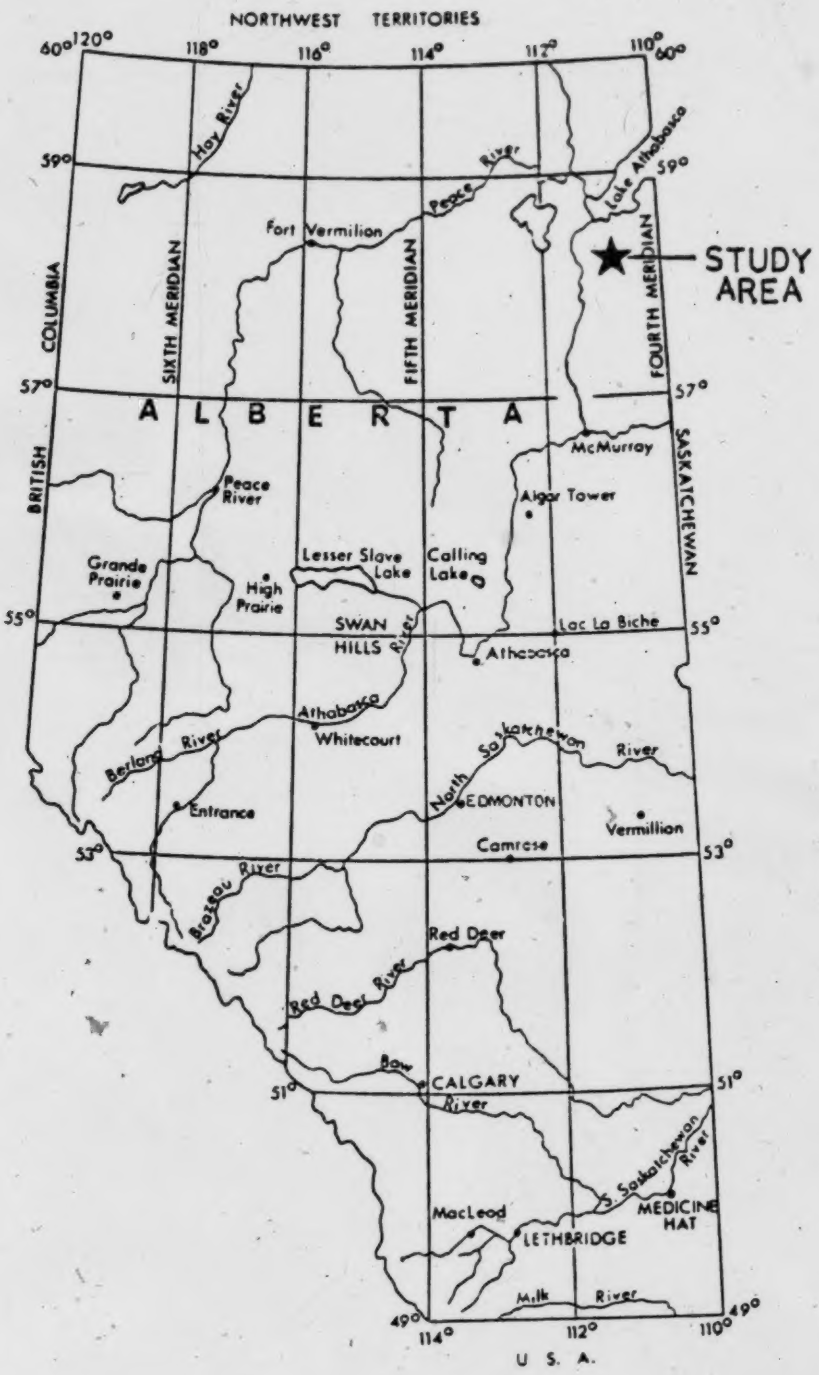
NORTHWEST TERRITORIES
60°
120°
118°
116°
114°
112°
110°
60°
Hay River
59°
Peace River
Lake Athabasca
59°
Fort Vermilion
STUDY AREA
COLUMBIA
SIXTH MERIDIAN
FIFTH MERIDIAN
FOURTH MERIDIAN
57°
A L B E R T A
57°
BRITISH
McMurray
SASKATCHEWAN
Peace River
Algar Tower
Grande Prairie
Lesser Slave Lake
Calling Lake
High Prairie
55°
SWAN HILLS
River
Lac La Biche
55°
Athabasca
Athabasca
Whitecourt
Berland River
North Saskatchewan River
EDMONTON
Entrance
Vermillion
53°
Camrose
53°
Brazeau River
Red Deer
Red Deer River
Bow
CALGARY
51°
River
51°
S. Saskatchewan River
MEDICINE HAT
MacLeod
LETHBRIDGE
Milk River
49°
114°
112°
110°
49°
U. S. A.

Figure 1 Location of study areas in Alberta (★).

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Plate 3 Aerial photograph of the paleo-parabolic dune on which the Blowout study site (○) was located. Scale is 1:40,000.

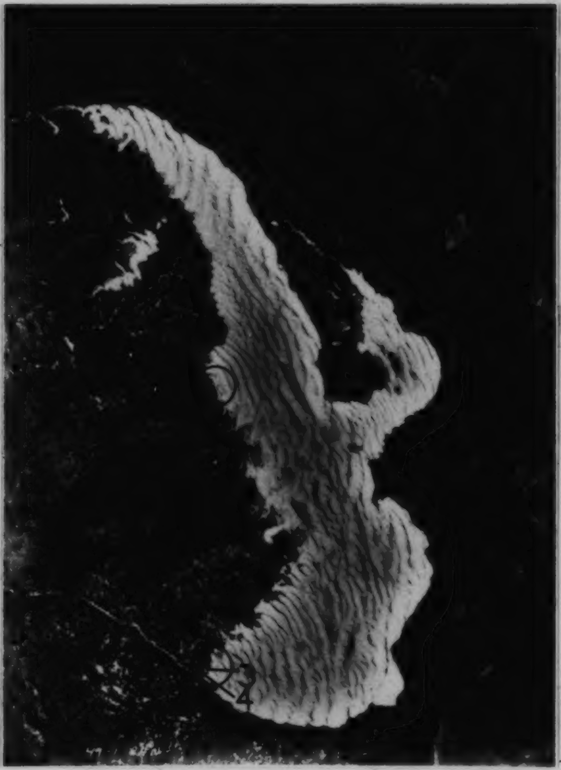

Plate 4 Aerial photo of Maybelle River Dune System. The location of the mid-dune and southern transects (○), and the meteorological stations (M_3 and M_4) are indicated. Scale 1:40,000.

Year round meteorological observations have been made at two locations close to the study area, Embarras (lat. 58°12', long. 111°23', observations from 1943 to 1962) and Fort Chipewyan (lat. 58°46', long. 111°07', observations from 1962 to present). Summer time (May to September) observations have been made at Keane Fire Tower (lat. 58°19', long. 110°17', observations since 1964) and Richardson Fire Tower (lat. 57°55', long. 110°58', observations since 1960). Due to the lack of data for calculations of longterm normals (currently based on the years 1941-1970 by Environment Canada), Longley and Janz (1978) have computed normals for these sites for the time period 1958-1976 (Table 1 and 2). In these calculations, data available from these sites are compared to Fort McMurray, correlation factors are determined and then applied to the Fort McMurray data in order to create calculated values for these sites. These data are then used for calculation of normals.

The climates of Fort Chipewyan and Embarras are quite different (Table 1), but will be used to represent the entire study area. Based upon NORMS, the microclimate is cold temperate; mean temperature of the warmest month (July) is 16.5 to 17.3°C, and the coldest month (January) is -22.4 to -26.4°C. Annual mean temperatures range from -1.1 to -2.8°C with approximately 140-150 frost-free $d.yr^{-1}$. Frosts may occur at anytime, and the average frost-free period at Fort McMurray lasts from June 15 to August 24 or approximately 69 consecutive days (Longley and Janz, 1978). There are an average of 20 to 25 d with frost from May to September inclusive. Annual degree

Table 1. Monthly temperature and precipitation NORMS for Fort Chipewyan (b) and Embarras (a). Normals based on Longley and Janz (1978) for the years 1958 - 1976. Degree days calculated as mean monthly temperature -5°C multiplied by number of days in the month.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Mean Annual	Total Annual	Total May to Sept	Total May to Aug
Mean monthly-maximum temperature (°C)																
a	-16.9	-12.7	-3.9	6.2	15.1	20.5	23.7	21.8	14.4	6.9	-4.8	-13.6	4.7	-	-	-
b	-20.7	-15.5	-7.2	3.2	13.4	19.4	22.6	20.8	13.1	5.5	-6.3	-14.5	2.8	-	-	-
Mean monthly minimum temperature (°C)																
a	-27.9	-25.6	-18.4	-6.9	2.0	7.3	10.8	9.2	4.2	-2.1	-13.2	-23.2	-7.0	-	-	-
b	-31.7	-27.7	-20.2	-8.6	1.2	7.2	10.3	8.6	3.3	-3.8	-14.7	-24.3	-8.4	-	-	-
Mean monthly mean temperature (°C)																
a	-22.4	-19.1	-11.2	-0.4	8.6	13.9	17.3	15.5	9.3	2.4	-9.0	-18.3	-1.1	-	-	-
b	-26.2	-21.6	-13.7	-2.7	7.3	13.3	16.5	14.9	8.2	0.9	-10.5	-19.4	-2.8	-	-	-
Number of days with frost																
a	31	28	31	25	11	2	<1	1	6	21	29	31	-	216	20	14
b	31	28	31	27	13	2	<1	1	9	23	30	31	-	226	25	6
Degree days >5.0°C.																
a	0	0	0	0	112	267	381	326	129	0	0	0	-	1215	1215	1086
b	0	0	0	0	71	249	357	307	96	0	0	0	-	1080	1080	984
Total precipitation (mm)																
a	10	9	14	14	36	53	73	52	52	25	22	11	-	371	266	214
b	23	15	22	21	26	45	59	45	42	26	23	21	-	368	217	175
Number of days with precipitation																
a	11	10	9	7	7	10	10	10	10	9	12	11	-	116	47	37
b	6	5	6	4	5	7	8	8	7	6	6	6	-	74	35	28
Mean monthly wind speed (km·hr^{-1})																
a	10.3	9.8	10.1	11.9	12.4	11.1	11.0	10.5	11.9	12.2	11.4	10.3	11.4	133	-	-

Table 2. Summer temperature and precipitation from 1976 to 1979 for Fort Chipewyan (a), Keane Fire Tower (b) and Richardson Fire Tower (c). Normals based on Longley and Janz (1978) for the years 1958-1976. Data source for 1976-1979 is Monthly Record of Meteorological Observations. Degree days are calculated as mean monthly temperature -5ºC multiplied by the number of days in the month. In April, degree days are the sum of daily mean temperature -5ºC. Incomplete data (*), no data available (-), trace precipitation (+) are indicated.

	April					May					June				
	Norm	1979	1978	1977	1976	Norm	1979	1978	1977	1976	Norm	1979	1978	1977	1976
Mean monthly temperature (°C)															
a	-2.7	-4.9	-1.5	1.9	4.6	7.3	5.8	7.3	10.4	10.2	13.1	13.5	13.2	14.0	14.2
b	-	-	-	-	-	8.6	7.6	8.4	13.0*	11.8	13.9	14.9	14.1	15.3	-
c	-	-	-	-	-	8.6	8.4	9.7	13.1	11.2	14.3	15.3	14.8	15.8	-
Numbers of days with frost															
a	27	29	25	24	20	13	17	9	4	7	2	2	4	1	0
b	-	4*	2*	-	-	-	13	10	1*	6	-	0	0	0	-
c	-	8*	1*	3*	-	-	12	8	1	6	-	0	0	0	-
Degree days >5.0°C															
a	0	0	8	38	0	71	25	71	167	161	249	255	246	270	276
b	-	0*	-	-	-	112	81	106	248*	211	267	297	273	309	-
c	-	0*	35*	45*	-	112	105	146	254	192	279	309	294	324	-
Total precipitation (mm)															
a	21	28	33.8	4.3	7.6	26	9.4	19.4	9.6	23.6	45	17.6	56.3	84.9	64.8
b	-	0.7*	0.6*	-	-	28	4.5	47.1	27.7*	51.6	55	13.4	44.3	75.4	-
c	-	4.1*	T*	4.0	-	26	8.8	38.8	57.5	35.6	54	38.9	51.1	43.7	-
Number of days with precipitation plus days with trace amounts															
a	4	12+11	8+4	5+3	4+4	5	4+4	10+6	5+7	10+4	7	11+4	12+3	8+7	12+1
b	-	1+1	1*	-	-	-	6+3	9+1	9+2*	11+3	-	8+3	13+4	14+3	-
c	-	2+3*	4*	1*	-	7	6+7	9+10	12+2	11+6	11	12+3	14+4	13+2	-

	July					August					September				
	Norm	1979	1978	1977	1976	Norm	1979	1978	1977	1976	Norm	1979	1978	1977	1976
Mean monthly temperature (°C)															
a	16.5	18.2	14.2	14.6	16.8	14.9	13.2	13.2	10.8	16.3	8.2	9.3	8.5	9.5	10.2
b	16.6	19.4	15.3	15.2	-	14.9	14.5	-	11.2	-	-	-	-	-	-
c	17.1	20.2	15.9	15.7	-	15.4	14.6	14.3	11.9	-	8.8	-	9.3*	-	-
Numbers of days with frost															
a	<1	0	0	0	0	1	1	0	2	-	9	1	4	4	5
b	-	0	0	0	-	-	0	-	0	-	-	-	-	-	-
c	-	0	0	0	-	-	0	0	0	-	-	-	-	-	-
Degree days >5.0°C															
a	357	409	285	298	366	307	254	254	180	350	96	133	105	135	156
b	360	446	319	316	-	307	296	-	192	-	-	-	-	-	-
c	375	471	338	332	-	322	298	288	200	-	114	-	108*	-	-
Total precipitation (mm)															
a	59	86	41.1	97.7	84.6	45	26.8	61.9	54.2	31.0	42	52.6	97.7	10.8	27.2
b	58	63.5	64.2	88.4	-	71	15.6	22.9*	81.9	-	68	-	-	-	-
c	61	57.6	37.3	87.6	-	59	58	47.9	46.9	-	43	-	89.1*	-	-
Numbers of days with precipitation plus days with trace amounts															
a	8	8+4	15+2	14+3	17+2	8	11	11+1	15+6	9+2	7	13+2	14+5	8+8	9+3
b	-	9+7	14+5	12+3	-	-	11+1	5+2	17+2	-	-	-	-	-	-
c	13	13+4	14+5	13	-	10	16+1	14+3	15+2	-	11	-	11+1	-	-

days range from 1080 to 1215 and are restricted to May through September Total precipitation is approximately 370 mm with the majority occurring in May to September inclusive (60% to 70% of total). There is a rapid rise in monthly precipitation from April to the maximum in July and a rapid decline from September to October. There are 35 to 47 d with measurable precipitation from May through September Mean annual wind speed is 11.4 km.hr^{-1} with a slightly windier May and October.

Within this study region, significant differences in microclimate occur between May and September inclusive. Calculated NORMS of Longley and Janz (1978) indicate that Richardson Fire Tower has a greater amount of precipitation, number of days with precipitation, degree days and is warmer than Keane Fire Tower and Fort Chipewyan (Table 2).

Based upon soil temperature and soil moisture regimes, Clayton et al., (1977) have classified the land region as Cryoboreal (mean annual soil temperature 2 to 8°C, mean summer soil temperature 8 to 15°C, growing season 120-220 d, 555 to 1250 degree-d above a 0°C base, and humid (showing slight moisture deficit) to sub-humid (showing significant moisture deficit, especially for higher lying sandy areas).

The study sites are situated on glacial deposits of sand and gravel which overlie the Physiographic Region-Athabasca Plain. The deposits originate from the Athabasca Formation (medium to coarse grained sandstone) and from Precambrian granitic plutonic rocks; both were eroded during the last glacial period by the Keewatin centered ice sheet. Aeolian reworking of the deposits since that time has resulted in a variety of active and revegetated dune forms, varying in shape, size, orientation and origin (Bayrock, 1969 and 1970).

Raup and Argus (1982) and David (1977, 1981) point out the confusion over proper classification of these sand dune areas in northern Saskatechewan and northeastern Alberta. The interpretation of these authors will be used and the differing terminologies of Tremblay (1961), Sproule (1939), Smith (1978), Hermesh (1972), and Rowe and Hermesh (1974) largely ignored.

David's interpretation of sand dune origin, formation and activity at the Cree Lake sand ridge formation in northwestern Saskatechewan is suitable for the Blowout site (David 1977, and 1981). He concludes that southeasterly adiabatic winds blowing off the retreating ice sheet were responsible for the aeolian reworking of deposits between 10800 and 8800 BP. These paleo-winds resulted in parabolic dune features including long parallel border ridges. The border ridges originated from the northwesterly elongation of the primary parabolic dune and vary in length up to 8 km. David (1981) concludes that the retreat of the ice sheet followed by movement of arctic air masses into the region resulted in southwesterly crosswind deformation and quasi-stabilization coinciding with vegetative stabilization. Landals (1978) hypothesizes that preservation of these features to the present is encouraged by the extensive wet, low-lying areas between the dune ridges (prevents ease of fire spread and improves the level of the water table under the ridges thereby aiding plant growth). The Blowout site was located on the more southern ridge of one of these so called paleo-dunes. David (1981), Landals (1978) and Raup and Argus (1982) conclude that these are unique sand dune features of considerable geomorphic interest.

Raup and Argus (1982) and Landals (1978) have intensively studied the large active dune field, called the Maybelle River Dune System. This dune field consists of two large coalescing parabolic dunes moving in a southeasterly direction leaving behind a revegetating flat sandy plain. The origin of the northern dune can be traced westward approximately 10 km to the Richardson River. The dune field consists of a variety of dune forms. There are a series of transverse ridges (oriented at right angles to the direction of the effective wind and concave to windward) separated by ventifacted gravel pavement (accumulation of pebbles and cobbles concentrated by wind removal of finer sand grains). These transverse ridges are of varied amplitude and wavelength, both decreasing in size towards the western edge of the dune field. Larger oblique ridge dunes have a shallow parabolic shape in plain view and are convex to the northeast with slip faces on the southeast side. Precipitation ridges are located on the eastern and southern edges of the dune field actively burying the forest and lakes. Within the dune field are a series of wet dune slacks (flat interdunal troughs). The Dune sites were located on the revegetating flat sandy plain along the western edge of the dune field.

The purpose of this investigation was to further characterize the physical nature of the two study sites, especially in terms of soil and microclimatological parameters.

MATERIALS AND METHODS

Soils

Soil pits were dug and the soils classified according to the Canadian System of Soil Classification (1978).

Soil samples were collected for analyses by the Soil and Feed Testing Laboratory, (Alberta Agriculture, Edmonton, Alberta). Cores were taken (10 cm diam x 10 cm) at 0-10 cm, 10-20 cm and 20-30 cm depths, placed in paper bags and air dried. In some cases the cores were taken through Hudsonia mats. In this case only the below ground portions of Hudsonia were left in the core.

Soil water determinations were done in a variety of ways. Most often cores, (10 cm diam. x 10 cm) were taken at depths of 0-10 cm, 10-20 cm and 20-30 cm, and placed in plastic bags for fresh weight determination. Samples were then air dried until no aggregations of sand grains were present and then reweighed for dry weight. Care was taken to ensure that plastic bags were not punctured. Preliminary investigations indicated that this method of sample handling and drying to constant weight was comparable to samples which were oven dried at 90°C for 24 hr. This was possible as the samples contained insignificant amounts of organic matter, such that with gentle mixing the samples air dried relatively quickly (1-2 d depending on weather conditions). Samples were weighed on an Ohaus Dial-O-Gram balance to the nearest 0.01 g.

Occasionally a smaller sample size was required for soil moisture determinations, as in the case of the 1978 plant water relations studies. In this instance, the barrel and plunger of a 50 ml disposable hypodermic syringe was used to collect the sample. Soils were collected at depths of 0-5, 5-10 and 10-15 cm and placed in tins for weight determination. These samples were weighed on a Mettler H10 balance to the nearest 0.001 g and oven dried at 60°C to constant weight.

Climate

Microclimatic data were collected at the Blowout site in 1977 and 1978, and at the Dune site in 1978. These data were compared to the Monthly Record of Meteorological Observations, and to Canadian Normals (1941-1970); both published by Atmospheric Environment, Dept. of Fisheries and Environment Canada. Data were compared with observations reported for Richardson Fire Tower and Fort Chipewyan. In addition, the microclimatic data collected by AOSERP project VE6.1 (located at Richardson Fire Tower) were used for comparison.

Temperature and relative humidity were recorded with a Belfort Hygrothermograph. Total solar radiation was recorded with a Belfort Actinograph, calibrated against an Eppley pyranometer and leveled with the slope. Daily temperature maxima and minima were recorded with a Taylor Max-Min thermometer. The hygrothermograph and Max-Min were housed in a shelter (each was 10 cm above the ground) and the actinograph was placed on top of the shelter (50 cm above ground).

The shelter was constructed according to Vogel and Johnson (1965). Due to the nature of the microhabitat, micrometerological observations were made with the shelter at ground level. Wind speed was measured with a Belfort 3-cup anemometer with the cups placed 1 m above ground level. In the case of more refined measurements, for example, in the plant water relations studies, a Hastings uni-directional hot wire anemometer was used. Precipitation was recorded using Taylor clear view rain gauges placed at a 50 cm height. A small amount of mineral oil was placed in all rain gauges to prevent evaporation. Soil and air temperature profiles were determined by a 24 point Grant thermistor probe recorder. Air probes were shielded from direct sunlight and placed at heights of 50, 10 and 2 cm. Soil probes were placed at 2, 10, 20 and 70 cm.

All temperature and relative humidity instruments were calibrated prior to, during, and after field use. During field use a Bacharach sling psychrometer was used for calibration. In the laboratory, electronically referenced calibrated thermocouples and an Assham Wet-Dry Bulb Thermometer were used.

Hygrothermograph data were digitized by Computing Services, University of Alberta. Hygrothermograph data points were read at 3 per hr and averaged. The hourly mean was recorded for temperature and relative humidity. Vapor pressure deficits were calculated from the hourly mean temperature and relative humidity after Lowe (1977). Actinograph data were digitized at 2 readings per hr. Total daily radiation was determined from the area under the curve calculations for 48 readings per 24 hr. Daily and monthly means, total and other calculations were made according to the Manual of Surface Weather Observations (MANOBS), unless otherwise stated.

Micrometerological observations at the Blowout were made at the center of the Blowout in a Hudsonia-sand community (M1-Fig. 2) and on a revegetated ridge top (approximately 100 m from the center of the Blowout) in a Hudsonia-lichen community (M2-Fig. 2). Observations at the Maybelle River Dune System were made at the southwestern part of the dune field in a Hudsonia-sand community (M3-Plate 4) and 300 m west from this location in a Pinus-lichen community (M4-Plate 4). Shielded max-min temperature readings were also taken on the open dune and in the Pinus-lichen community to the southeast of the dune field, at 10 cm above the ground.

Fire history was determined by tree coring and tree wedge collecting from trees with obvious fire scars. Cores were mounted, counted and deposited in the Botany Department Core Collection. Tree ages for non-fire scarred trees were similarly recorded.

Rates of sand deposition and deflation, and dune and blowout movements were recorded in a number of ways. Wooden stakes were placed at 15 m intervals around the perimeter of the Blowout. Deflation and deposition were recorded as change in sand height from original sand height, and Blowout movement was recorded as distance from stake to leading edge at the base of the Blowout. Dune movement at the dune field was determined by using 1976 Alberta Ecological Survey markers and the 1974 Landals (1978) markers. Dune movement was recorded as distance from marker to base of dune perimeter.

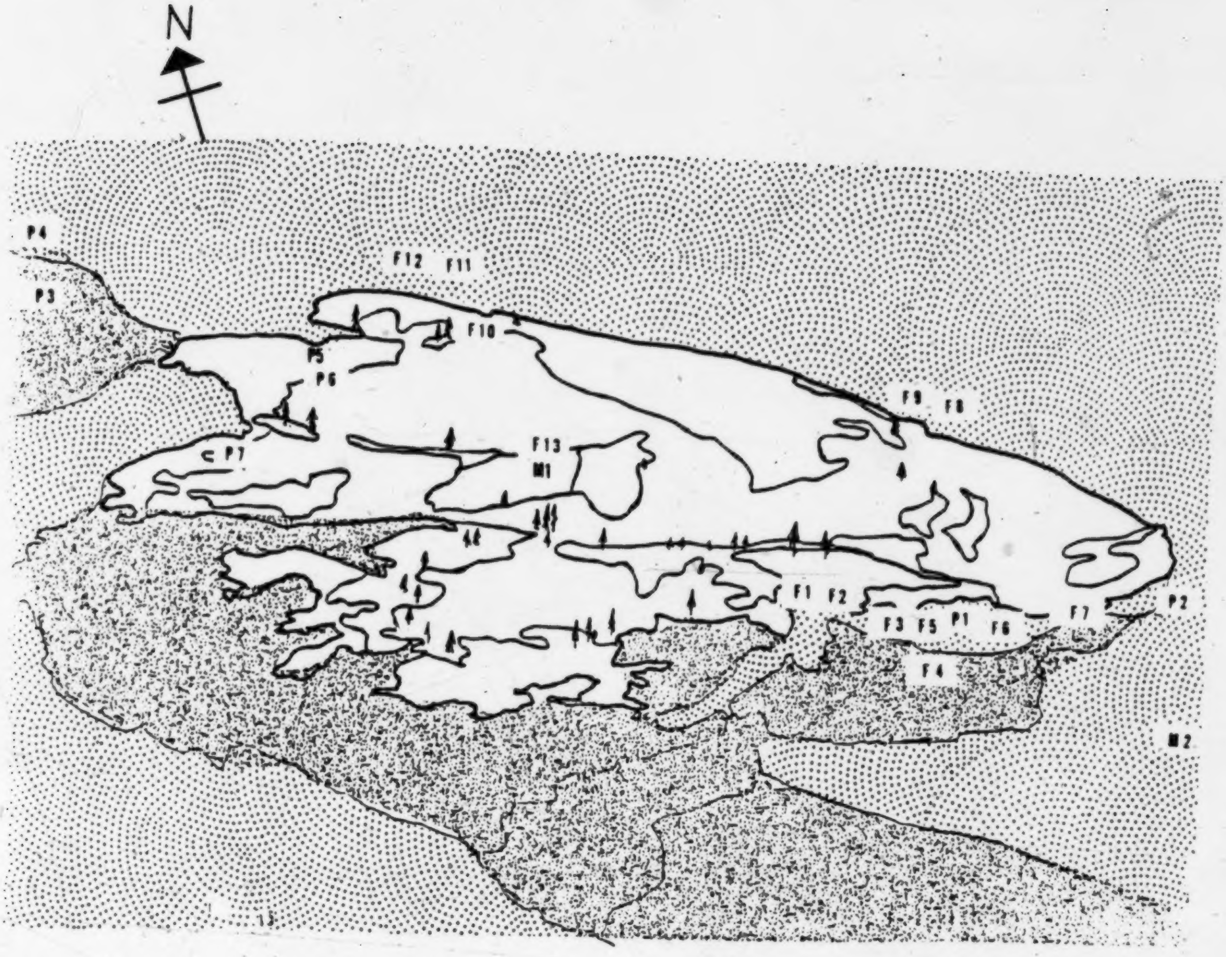
N
P4
P3
F12
F11
F10
P5
P6
P7
F13
M1
F9
F8
F1
F2
F3
F5
P1
F6
F7
P2
F4
M2

Figure 2 Location of meteorological stations (M), soil pits (P), cored trees (F) and plant communities at the Blowout site. Plant communities include: *Hudsonia*-lichen community (▨), *Hudsonia*-sand community (▭), *Pinus*-lichen woodland (⁙), and isolated trees of *Pinus* (↟).

Sand deposition and deflation were also measured for microhabitats at both the Dune and Blowout sites. Glass slides (7.5 x 2.5 x 0.1 cm) were inserted horizontally into the ground at a depth of approximately 5.0 cm. A metal rod (2 mm diam.) was permanently inserted vertically at one end of the glass slide. Depth to glass slide measurements were made at a distance of 5 cm in a defined direction from this metal rod by inserting a pointed rod (1 mm diam.) into the sand. The rod was scored at sand surface, retracted and measured with a 10 cm ruler. A glass slide was inserted into a stable Hudsonia-Polytrichum piliferum community for calibration purposes.

RESULTS

Climate

At Richardson Fire Tower between May and August inclusive; 1976 was warmer (+5.7°C), and wetter (+27.4 mm), 1977 was warmer (+1.1°C) and wetter (+34.7 mm), 1978 was slightly cooler (-0.7°C) and slightly drier (-14.9 mm), and 1979 was warmer (+3.1°C and drier (-36.7 mm) than NORMS (Table 3). In all years there were more days with precipitation than the NORM (1976 = +20, 1977 = +12, 1978 = +10, 1979 = +6).

Large deviations from NORMS include: hot May of 1976 and 1977, hot July 1979, cold August of 1977, wet May of 1977, wet September of 1978 and the dry September of 1977 (Table 3).

The Blowout experienced four more frosts in June of 1978 than Richardson Fire Tower. Comparison of precipitation data between

Table 3. Comparison of NORMS to Richardson Fire Tower micrometeorological observations from 1976 to 1979. Fort Chipewyan data were used when Richardson Fire Tower data were lacking (Sept. 1976-1979), mean monthly temperature (^{o}C), total precipitation (mm), and number of days with precipitation. A + indicates that Richardson Fire Tower data were greater than NORM, and a - that Richardson Fire Tower were less than NORM.

Year	Observation	May	June	July	August	September	May to August	May to September
1976	Mean temperature	+2.9	+1.0	+0.3	+1.4	+2.0	+5.7	+7.7
	Total precipitation	-2.4	+18.2	+25.6	-14.0	-15.2	+27.4	+12.2
	Number of days with precipitation	+5	+5	+9	+1	+2	+20	+22
1977	Mean temperature	+4.5	+1.5	-1.4	-3.5	+1.3	+1.1	+2.4
	Total precipitation	+31.5	-10.3	+26.6	-12.1	-31.2	+35.7	+4.5
	Number of days with precipitation	+5	+2	0	+5	+1	+12	+13
1978	Mean temperature	+1.1	+0.5	-1.2	-1.1	+0.3	-0.7	-0.4
	Total precipitation	+12.8	-2.9	-23.7	-11.1	+55.7	-14.9	+40.8
	Number of days with precipitation	+2	+3	+1	+4	+7	+10	+17
1979	Mean temperature	-0.2	+1.0	+3.1	-0.8	+1.3	+3.1	+4.4
	Total precipitation	-17.2	-15.1	-3.4	-1.0	+10.4	-36.7	-26.3
	Number of days with precipitation	-1	+1	0	+6	-2	+4	+4

Richardson Fire Tower and the Blowout indicated variability in amounts of rainfall and in the number of precipitation days. The Blowout had slightly more days of rain than did Richardson Fire Tower.

Mean monthly air temperatures, number of days with frost, degree days, total precipitation and number of days with precipitation for the Blowout study sites were similar to each other (Table 4). Paired statistical analysis (Table 5) of mean daily air temperatures, from May to August inclusive, indicated that in 1977 the Hudsonia-sand community was significantly warmer with a difference between means of 0.4°C. In 1978 the difference between means was only 0.2°C and not significant. Combined 1977 and 1978 daily means were not significantly different between the two study sites, both having a combined May to August inclusive mean daily air temperature equal to 15.4°C. Similar analysis of maximum daily temperature indicated that the Hudsonia-sand community was significantly cooler than the Hudsonia-lichen community (1977 cooler by 0.7°C, 1978 cooler by 1.2°C and in 1977-1978 combined, cooler by 1.0°C). On the other hand, the minimum daily temperature was significantly warmer (1977 warmer by 1.5°C, 1978 warmer by 0.7°C and in 1977-1978 combined, warmer by 1.2°C).

A comparison of air and soil temperature profiles between a Hudsonia-sand community with and without standing dead indicated that the soil temperature at 10 cm, 1 cm and 0 cm was significantly higher for the community without standing dead over a 24 hr period (Table 6). These profiles showed diurnal variability on a representative

Table 4. Temperature, precipitation, radiation, wind and vapor pressure deficit (VPD) summaries for Hudsonia-sand (a) and lichen (b) communities at the Blowout site, 1977 and 1978.

	May		June		July		August		May to August		
	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978	1977/78
Mean monthly temperature (^{o}C)											
a	13.0	12.1	16.0	16.2	16.3	16.3	12.6	15.9	14.5	15.1	14.8
b	13.1	12.4	16.3	16.1	15.9	16.8	12.0	16.5	14.3	15.5	14.9
Numbers of days with frost											
a	1	3	0	4	0	0	1	0	1	2	1
b	1	3	0	4	0	0	1	0	1	2	1
Degree days (>5^{o}C)											
a	248	220	330	333	350	350	236	338	1164	1241	2405
b	251	229	339	336	338	367	217	357	1145	1289	2434
Total precipitation (mm)											
a	-	20.3	15.5	65.7	64.8	40.1	49.5	35.2	130	161	291
b	-	19.3	15.5	64.8	64.0	39.6	49.3	34.6	129	158	287
Number of days with precipitation											
a	-	7	15	18	15	19	13	13	48	62	-
b	-	7	15	18	15	19	13	13	48	62	-
Number of observations : temperature and precipitation											
n	10	9	12	29	31	30	16	20	69	88	157
Number of days with morning dews, heavy dews											
a	-	4,4	-	26,7	-	22,11	-	17,12	-	69,34	-
Mean monthly wind speed km.hr^{-1}											
a	-	4.49	6.00	3.61	4.47	5.39	4.51	5.10	4.78	4.64	4.70
b	-	3.09	3.59	3.33	2.96	3.78	3.52	3.25	3.27	3.44	3.37
Number of days of observation : wind											
a	-	10	13	30	31	31	23	20	67	91	158
b	-	10	13	30	31	31	23	20	67	91	158
Mean monthly total daily radiation (MJ.m^{-2})											
a	-	17.8	21.1	21.4	19.6	21.1	16.4	16.9	19.0	19.8	19.4
b	-	14.3	17.8	19.4	17.9	18.9	15.5	16.6	17.4	18.1	17.8
Number of days of observation : radiation											
a	-	9	23	29	30	27	25	20	78	85	163
b	-	8	15	29	31	27	20	20	66	84	150
Daily mean VPD (KPa)											
a	4.04	2.96	6.22	4.87	5.52	4.65	3.88	3.18	4.98	4.23	4.59
b	6.08	3.00	6.27	4.84	5.84	4.55	4.06	3.21	5.45	4.18	4.84
Number of days of observation : VPD											
a	9	6	11	28	30	26	16	19	66	79	145
b	9	6	11	28	30	26	16	19	66	79	145

Table 5. Statistical comparison of micrometeorological parameters between Hudsonia-sand (a) and lichen (b) communities at the Blowout site, 1977 and 1978. Paired 't' analysis a vs b.

	May		June		July		August		May to August		
	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978	1977/78
Daily mean temperature											
t	-2.12	-1.42	4.77	0.45	5.81	0.50	1.63	-6.56	2.81	0.45	1.62
df	9	8	11	28	30	29	15	19	68	87	156
95%	2.26	2.31	2.20	2.05	2.04	2.05	2.13	2.09	1.99	1.99	1.98
Daily maximum temperature											
t	-5.04	-3.74	-5.47	-7.12	-4.81	-7.08	-2.28	-7.95	-7.37	-13.09	-14.19
df	9	8	11	28	30	29	16	19	69	87	157
95%	2.26	2.31	2.20	2.05	2.04	2.05	2.12	2.09	1.99	1.99	1.98
Daily minimum temperature											
t	1.62	2.05	6.19	7.52	9.59	3.86	7.70	1.91	11.31	7.64	12.78
df	9	8	11	28	30	29	15	19	68	87	156
95%	2.26	2.31	2.20	2.05	2.04	2.05	2.13	2.09	1.99	1.99	1.98
Daily wind speed											
t	-	6.23	7.89	8.63	7.62	10.08	4.98	8.89	-	-	-
df	-	9	12	29	30	30	22	19	-	-	-
95%	-	2.26	2.18	2.04	2.04	2.04	2.07	2.09	-	-	-
Total daily radiation											
t	3.63	3.46	4.87	3.11	2.82	5.14	.84	8.67	6.34	6.01	-
df	7	13	28	29	25	19	20	63	81	145	-
95%	2.37	2.16	2.05	2.05	2.06	2.09	2.09	2.00	1.99	1.98	-
Daily mean VPD											
t	-13.81	-0.22	-0.36	0.23	-5.89	0.64	-2.47	-64.4	-0.84	-4.30	
df	9	6	11	28	30	26	19	19	72	82	155
95%	2.26	2.45	2.20	2.05	2.09	2.06	2.09	2.09	1.99	1.99	1.98
Daily maximum VPD (KPa)											
t	-8.45	-0.38	-4.65	-1.86	-6.39	0.44	-4.65	-1.81	-9.24	-2.38	-7.09
df	9	6	11	28	30	26	19	19	72	82	155
95%	2.26	2.45	2.20	2.05	2.04	2.06	2.09	2.09	1.99	1.99	1.98
Daily minimum VPD (KPa)											
t	-7.68	2.82	0.12	2.11	-0.07	4.55	-0.69	3.28	-2.18	5.98	-1.60
df	9	6	11	28	30	26	19	19	72	82	155
95%	2.26	2.45	2.20	2.05	2.04	2.06	2.09	2.09	1.99	1.99	1.98

Table 6. Comparison of mean hourly soil and air temperatures between *Hudsonia*-sand communities without (a) and with standing dead (b). Comparison over one 24 hr period.

	Temperature (°C)			
	Profile ht (cm)			
Site	-10	-1	0	+10
a	16.56	18.78	19.62	17.48
b	16.86	18.02	18.27	--
t	2.64	2.07	2.18	--
df	23	23	23	--
95%	2.07	2.07	2.07	--

sunny day (Figs. 3 and 4). Soil temperature at 70 cm varied 0.6°C, lagging behind changes in air temperature. Soil temperature remained higher than air temperatures from approximately 2000 hr to 0700 hr Maximum temperature was located at and above soil surface from 0700 hr to 2000 hr. Air temperatures responded quickly to short cloudy periods whereas soil temperatures did not (Fig. 4).

Mean and minimum daily temperatures were significantly higher in the Pinus-lichen community along the western edge of the Maybelle River Dune System than in the open Hudsonia-sand community or in the Pinus-lichen community to the east of the advancing dune system (Table 7).

Mean monthly wind speed was significantly greater for the Hudsonia-sand community versus the Hudsonia-lichen community at the Blowout (Table 5). Combined 1977-1978 means for the Hudsonia-sand community were significantly greater by 1.3 km.hr^{-1}. A comparison of wind profiles between a Hudsonia-sand community with and without standing dead indicated that only at plant height was the wind speed significantly different (Table 8). In 1977, the community without the standing dead had the greater wind speeds; in 1978, the community with the standing dead had the greater wind speeds; and in 1977 plus 1978 combined, there was no significant difference. Wind speed and direction varied within the Blowout on an exceptionally windy day (August 9, 1977). Maximum wind speed at 1.3 m height was measured at 120 km.hr^{-1} along the northern edge of the Blowout, and at 64 km.hr^{-1} as the wind exited the Blowout. Daily wind speeds were

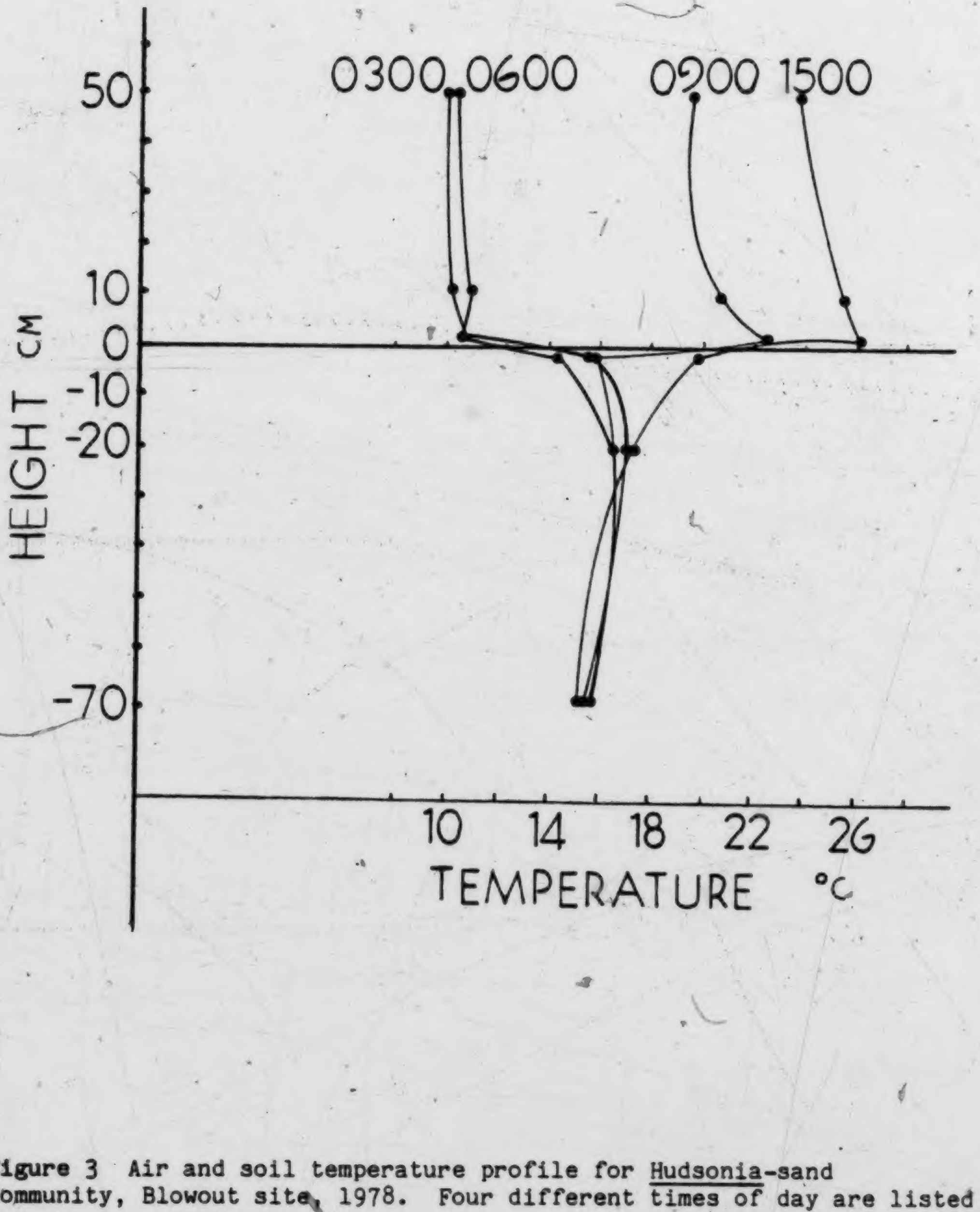

Figure 3 Air and soil temperature profile for Hudsonia-sand community, Blowout site, 1978. Four different times of day are listed for July 10, 1978.

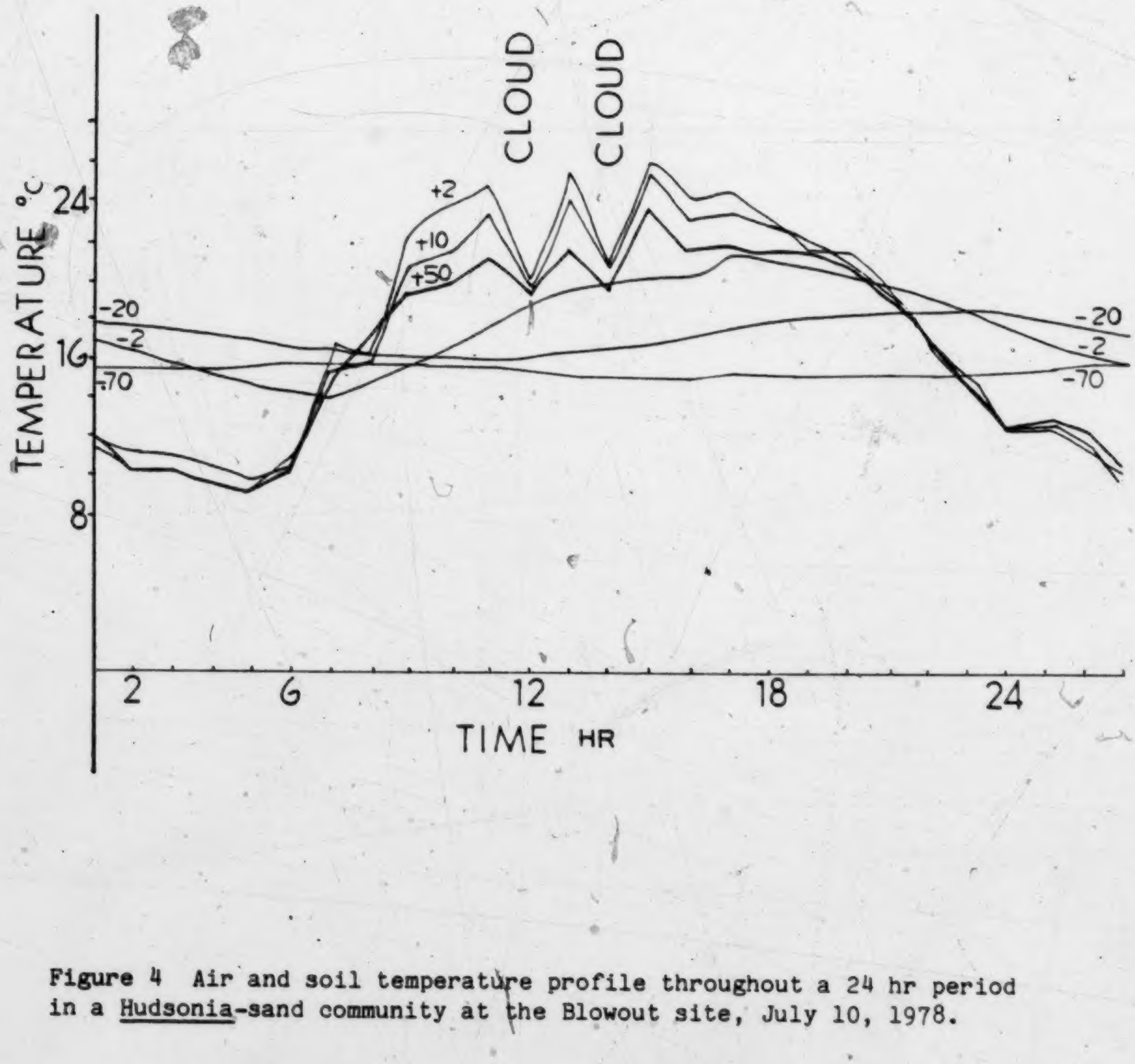

Figure 4 Air and soil temperature profile throughout a 24 hr period in a Hudsonia-sand community at the Blowout site, July 10, 1978.

Table 7. Comparison of microclimatological parameters between plant communities at the Maybelle River Dune System, 1978. Paired data analysed between the Pinus-lichen and Hudsonia-sand communities on the western edge (a) and between the Pinus-lichen communities on the eastern and western edge of the Maybelle River Dune System (b).

Site comparison	Daily mean temperature			Daily maximum temperature		Daily minimum temperature		Mean daily wind speed	
	t	df	95%	t	df	t	df	t	df
a	5.03	17	2.11	1.88	17	2.94	17	-6.99	17
b	3.71	6	2.45	1.94	6	4.82	6	--	--

Table 8. Wind profile in *Hudsonia*-sand communities without (a) and with (b) standing dead, Blowout site, 1977 and 1978. Spot readings were taken during summer, plant height in (a) equals 1-2 cm and 5-8 cm in (b).

Year	Height above ground	a		b		Paired a vs. b		
		$\bar{x}$	n	$\bar{x}$	n	t	df	95%
1977	70 cm	4.85	27	5.74	27	-0.77	26	2.06
	30	4.20	27	4.26	27	-0.09	26	2.06
	10	3.41	27	2.87	27	1.00	26	2.06
	plant	2.52	27	1.59	27	3.14	26	2.06
1978	30 cm	6.66	11	9.17	11	-1.66	10	2.23
	10	4.83	11	5.90	11	-1.24	10	2.23
	plant	2.09	11	3.50	11	-2.57	10	2.23
	0	1.50	11	2.15	11	-1.62	10	2.23
1977/ 1978	30 cm	4.91	38	6.86	38	-1.06	37	2.03
	10	3.83	38	3.75	38	0.16	37	2.03
	plant	2.39	38	2.14	38	0.74	37	2.03

significantly greater in the Hudsonia-sand community than in the Pinus-lichen community along the western edge of the Maybelle River Dune System (Table 7).

Mean total daily radiation was significantly greater for the Hudsonia-sand community versus the Hudsonia-lichen community at the Blowout (Table 5). The mean total daily radiation for May to August inclusive for combined 1977-1978 was 1.6 $MJ.m^{-2}$ greater.

Mean daily vapour pressure deficits were significantly greater for the Hudsonia-sand community versus the Hudsonia-lichen community at the Blowout (Table 5).

Soils

Soils on the Blowout site were mainly classified as Orthic Regosols. Evidence for past fires was found at varying depths within the Blowout. In the northern part of the Blowout, two buried charcoal horizons were found (Figs. 2 and 5). Based on changes in location of charcoal horizons in neighboring profiles (Fig. 5, P5 and P6), it is clear that, the main bowl of the present Blowout is below the soil level at which fires took place. Burial of charcoal may have taken place at the expense of bowl sands.

Soils of the Pinus-lichen communities surrounding the Blowout were classified as Orthic Eutric Brunisols and Eluviated Eutric Brunisols. Evidence of past fires was found at varying depths in these profiles (Fig. 5).

9

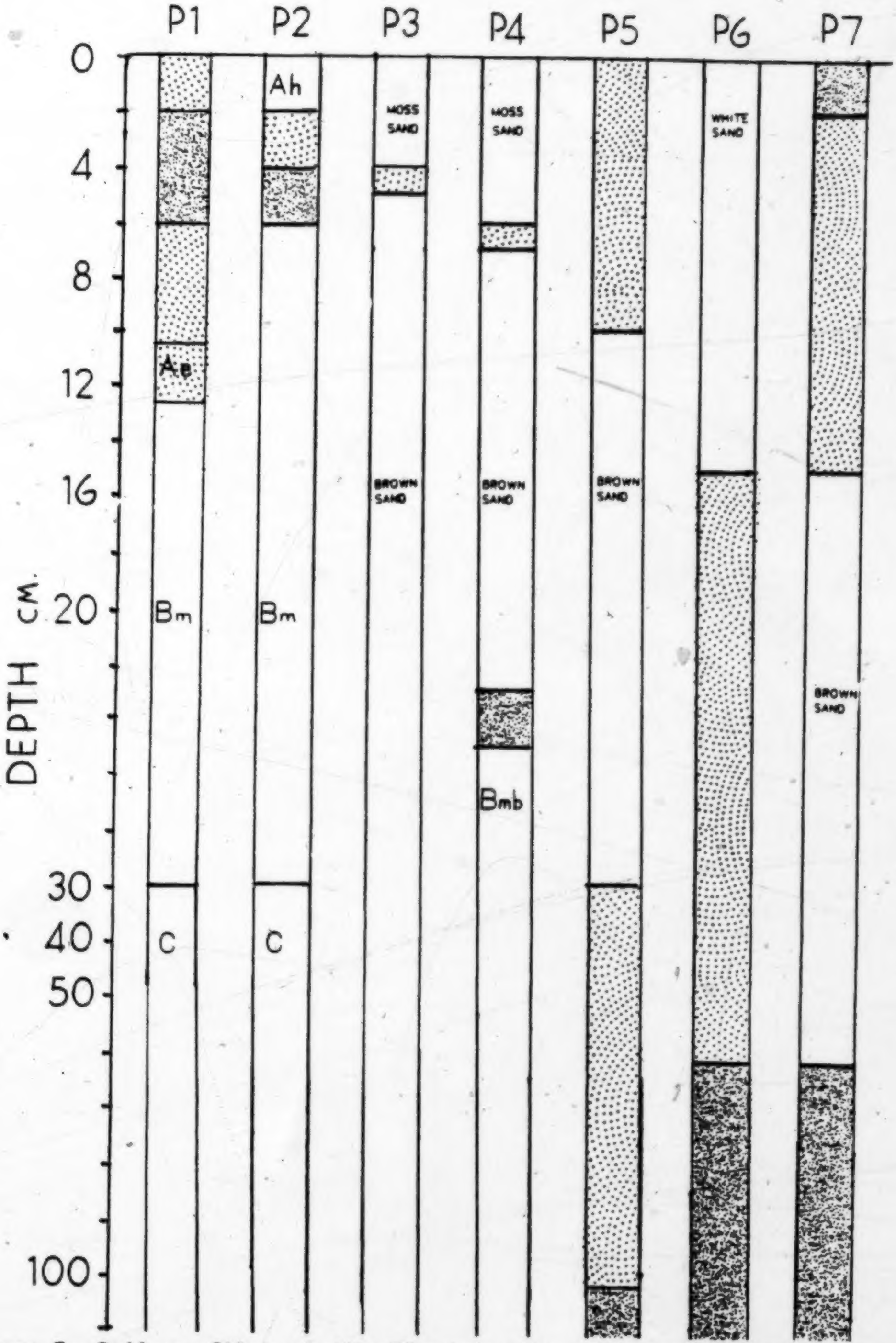
P1
P2
P3
P4
P5
P6
P7
DEPTH CM.
0
4
8
12
16
20
30
40
50
100
Ah
Ae
Bm
Bm
C
C
MOSS SAND
MOSS SAND
WHITE SAND
BROWN SAND
BROWN SAND
BROWN SAND
BROWN SAND
Bmb

Figure 5 Soil profiles at the Blowout site. Pits were dug under a P. banksiana/H. tomentosa/lichen community (P1), a P. banksiana/ Vaccinium myrtillodes/lichen community (P2), a H. tomentosa/ Polytrichum piliferum/lichen community (P3), a H. tomentosa/P. piliferum/sand community on a border ridge top (P4), and on open sand areas with surfical charcoal (P5, P6) and 2 m downslope (P7). Coarse heavy black charcoal remains ▓, and finer gray sand charcoal layers ░ are indicated.

Soil analyses of samples from the Dune site indicated that NO_3-N, K, Na, SO_4-S, organic matter, and conductivity were low (Table 9). Levels of PO_4-P were lowest in the Pinus-lichen community. No correlations with depth in the profile and nutrient content were detected. Further nutrient analyses were not attempted due to cost and questionable accuracy of results at such low concentrations.

Within the Blowout, considerable sand movement took place (Table 10). Mean deposition in Hudsonia communities for the time period August 28, 1977 to August 1, 1979 ranged from 3.5 $mm.yr^{-1}$ to 33 $mm.yr^{-1}$. For any time period of measure, maximum deposition ranged from 35 $mm.yr^{-1}$ to 47 $mm.yr^{-1}$ and maximum deflation ranged from 0 $mm.yr^{-1}$ to 17 $mm.yr^{-1}$. Only the wind sheltered slope showed continuous deposition. All other Hudsonia communities exhibited a cyclic deflational and depositional nature with an overall tendancy towards deflation. Communities without standing dead experienced more deposition than did those with aboveground standing dead.

A comparison of selected ridges and bowls within the Blowout to the perimeter of the Blowout indicated that mean deposition from August 19, 1977 to August 1, 1979 was similar (30.20 $mm.yr^{-1}$ versus 38.80 $mm.yr^{-1}$, respectively). The perimeter of Blowout showed continuous deposition with the maximum for any period equal to 117 $mm.yr^{-1}$. The selected bowls and ridges had cyclic deposition and deflation with a maximum deposition for any time period of 44 $mm.yr^{-1}$ and a maximum deflation for any period of 43 $mm.yr^{-1}$.

Depth (cm)	Pounds per acre					pH	Conductivity (mmhos)	Organic Matter
	NO_3-N	PO_4-P	K	Na	SO_4-S			
Pinus - lichen community								
0 - 10	1	10	14	L^-	L^+	5.7	0.2	L^-
10 - 20	0	12	7	L^-	L	5.7	0.2	L^-
20 - 30	0	12	4	L^-	L	5.7	0.2	L^-
Hudsonia - open sand community								
0 - 10	0	49	6	L^-	L^-	6.1	0.2	L^-
10 - 20	0	42	4	L^-	L	5.9	0.2	L^-
20 - 30	0	35	6	L^-	L	5.8	0.2	L^-
Open sand								
0 - 10	0	40	3	L^-	L	5.7	0.2	L^-
10 - 20	0	38	3	L^-	L^-	6.0	0.2	L^-
20 - 30	1	23	49	L	L^-	6.2	0.2	L^-
Through *Hudsonia* plant								
0 - 10	0	35	11	L^-	L	5.1	0.2	L^-
0 - 10	0	41	26	L^-	L	5.3	0.2	L^-

Table 9. Soil analyses from the Maybelle River Dune System. Samples contain 100% sand size particles. Low amounts are indicated as L, extremely low by L-.

Table 10. Sand movements within the Blowout site, 1977 and 1978. *Hudsonia*-sand communities without standing dead were located on a strongly depositional slope (a), a depositional ridge top (b), and on mid-Blowout slip (c), slope (d) and slope base (e). Measurements were also made on *Hudsonia*-sand communities with standing dead (f), *Hudsonia* - *Polytrichum piliferum* communities (g), around the Blowout perimeter (h) and on selected ridges and bowls within the Blowout (i).

	Amount.d^{-1} x 10^{-2} (mm)																		Amount.yr^{-1} (mm)		
	June 26, 1977 to Aug 28, 1977			Aug 28, 1977 to May 24, 1978			May 24, 1978 to Aug 17, 1978			Aug 28, 1977 to Aug 17, 1978			Aug 17, 1978 to Aug 1, 1979			June 26, 1977 to Aug 1, 1979			Aug 28, 1977 to Aug 1, 1979	For any time period	
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	Max.	Min.
	Hudsonia - sand community without standing dead																				
a	6.49	1.69	4	5.53	2.68	4	12.56	2.59	4	7.22	2.52	4	10.94	2.76	4	8.66	2.22	4	33.14	45.84	20.19
b	12.89	6.90	4	4.28	0.61	4	-1.94	1.35	4	2.78	0.17	4	3.99	1.04	4	4.17	0.83	4	12.35	47.05	-7.08
c	-1.90	4.61	7	2.42	0.70	7	5.08	8.05	7	3.05	1.63	7	5.03	1.95	7	3.52	1.92	7	14.75	18.54	-6.94
d	1.64	1.99	4	0.51	0.65	4	-1.71	1.90	4	-0.02	0.21	4	3.24	1.68	4	1.31	0.70	4	5.88	11.83	-6.24
e	1.76	2.79	4	-0.05	0.36	4	11.44	2.79	4	2.01	0.30	4	-0.10	0.42	4	1.35	0.50	4	3.49	41.75	-0.37
	Hudsonia - sand community with standing dead																				
f	-4.69	9.54	4	-1.39	1.18	4	0.97	1.26	4	-0.83	0.97	4	0.75	1.33	4	-0.45	1.25	4	-0.15	3.54	-17.12
	Hudsonia/Polytrichum piliferum community																				
g	0.53	2.00	3	0.37	0.19	3	-0.28	0.18	3	0.09	0.10	3	0.05	0.08	3	0.11	0.20	3	0.26	1.93	-1.02

	Amount.d^{-1} x 10^{-2} (mm)																		Amount.yr^{-1} (mm)		
	July 30, 1977 to Aug 19, 1977			Aug 19, 1977 to June 17, 1978			June 17, 1978 to Aug 21, 1978			Aug 19, 1977 to Aug 21, 1978			Aug 21, 1978 to Aug 1, 1979			July 30, 1977 to Aug 1, 1979			Aug 19, 1977 to Aug 1, 1979	For any time period	
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	Max.	Min.
	Blowout																				
h	9.33	8.20	13	6.93	1.47	13	32.08	7.15	13	11.95	2.57	13	9.31	3.15	8	12.27	3.18	8	38.80	117.09	25.29
i	-11.88	11.69	8	6.86	4.35	7	12.12	12.11	7	6.77	5.61	7	9.78	4.56	4	6.56	4.92	4	30.20	44.24	-42.36

The Hudsonia-Polytrichum community showed very little deflational or depositional activity; 0.26 mm.yr^{-1} from August 28, 1977 to August 1, 1979. The sampling site was located approximately 75 m from open sand. Maximum deposition for any period equalled 1.9 mm.yr^{-1}. These measures represented the error in the measurement technique and accounted for the compacting effect of recent rain drops and variations in soil moisture.

Maximal Blowout advancement into the surrounding forest took place at the southeastern (150 mm.yr^{-1}) and northeastern (58 mm.yr^{-1}) corners of the Blowout (Fig. 6 and Table 10).

A Hudsonia covered ridge extending into the open dune fields along the western edge of the Maybelle River Dune System showed variable sand deflation (wind exposed ridge top) and deposition (wind sheltered mid and base of ridge slope) (Table 11A, B, C). The overall tendency within these Hudsonia-sand communities was towards sand deposition (range from 4.9 mm.yr^{-1} to 35.5 mm.yr^{-1}).

A large Hudsonia plant located on a hummocked and hollowed ridge showed varied deposition (48.7 x 10^{-2} mm.d^{-1}) and deflation (17.8 x 10^{-2} mm.d^{-1}) on the wind sheltered and wind exposed side of the plant respectively (Table 11D, E).

A transverse dune, partially vegetated by grasses, showed varied amounts of sand deposition and deflation. Deflation varied from more than 90 mm.yr^{-1} at the foredune to 8.4 mm.yr^{-1} in old standing dead Agropyron smithii at the dune top (Table 11F-K). Living A. smithii on terraces encouraged greater amounts of deposition (69.4 to 77.5 mm.yr^{-1}) than in its absence (21.0 mm.yr^{-1}).

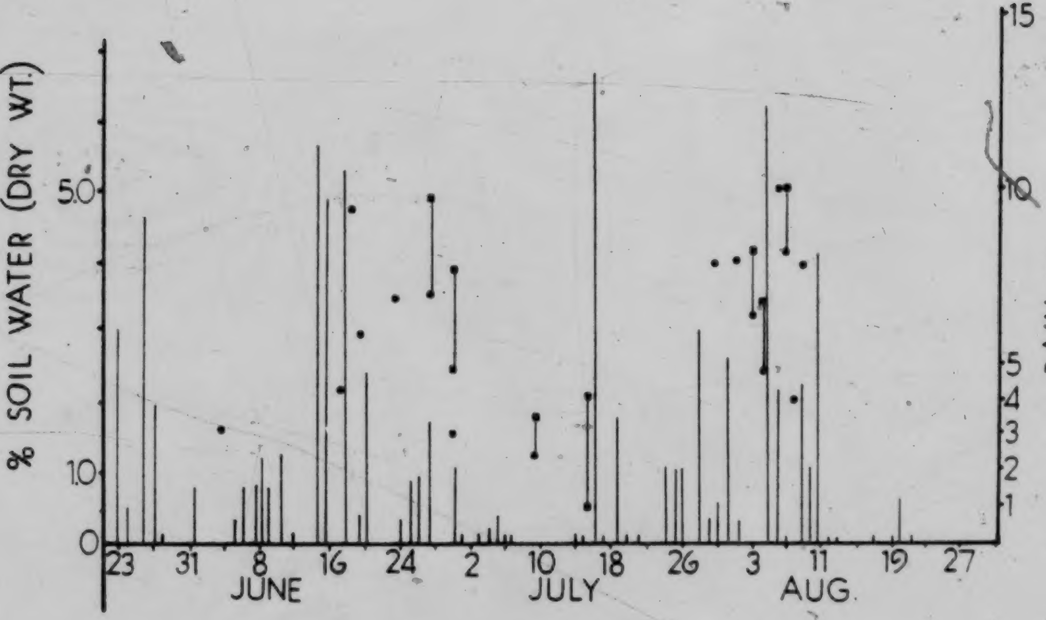

Figure 6 Selected soil water contents and precipitation summary for the Blowout site, 1978. Soil water content was sampled at a 0 to 30 cm depth in Hudsonia-sand community (●), and Hudsonia-lichen community (■). Connected soil water contents were paired in time. July 15 readings were from the western edge of the Maybelle River Dune System.

Table 11. Sand movements at the Maybelle River Dune System in 1978 and 1979. Measurements were made along the western edge of the dune system at the top (a), midslope (b) and base (c) of Hudsonia ridge, and on a large Hudsonia plant experiencing deflation (d) and deposition (e). Measures were also made on an Agropyron smithii inhabited transverse dune (for dune (f), ridgetop (g), and slope (j) and terraces (with (i) and without (h) Agropyron smithii). Perimeter measurement was made using the 1974 Landals markers (Landals 1978).

	Amount.d^{-1} (10^{-2} mm)															Amount.yr^{-1} (mm)		
	June 7, 1978 to Aug 22, 1978			July 17, 1978 to Aug 22, 1978			Aug 22, 1978 to Aug 5, 1979			June 7, 1978 to Aug 5, 1979			July 17, 1978 to Aug 5, 1979			Aug 22, 1978 to Aug 5, 1979		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Hudsonia sand ridge																		
a	-3.16	-	1	-	-	-	1.33	-	1	-1.66	-	1	-	-	-	4.86	-	1
b	20.40	-	1	-	-	-	9.65	-	1	11.58	-	1	-	-	-	35.22	-	1
c	11.18	-	1	-	-	-	8.70	-	1	9.15	-	1	-	-	-	31.76	-	1
Large Hudsonia plant on ridge top																		
d	-17.76	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
e	48.68	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Agropyron sand ridge; mid-dune field																		
f	-	-	-	-5.14	-	1	<-15.0	-	1	-	-	-	<-25.0	-	1	<-90.0	-	1
g	-	-	-	-10.81	23.3	2	-1.39	4.04	2	-	-	-	-2.30	1.41	2	-8.38	5.13	2
h	-	-	-	45.27	12.03	2	1.55	0.64	2	-	-	-	5.76	1.73	2	21.0	6.31	2
i	-	-	-	93.70	33.3	6	15.0	1.83	6	-	-	-	21.67	3.07	6	77.5	7.39	6
j	-	-	-	87.84	-	1	8.79	-	1	-	-	-	16.41	-	1	69.4	-	1

	Amount.d^{-1} (10^{-2} cm)									Amount.yr^{-1} (cm)		
	June 3, 1978 to Aug 22, 1978			Aug 22, 1978 to Aug 4, 1979			June 3, 1978 to Aug 4, 1979			Aug 22, 1978 to Aug 4, 1979		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Perimeter of Dune Field, 1974 Landal Markers												
Mean	74.4	16.87	11	15.19	4.16	10	29.77	6.88	9	60.99	15.8	9
Max.	190.0	-	1	43.23	-	1	70.73	-	1	157.79	-	1
Min.	10.0	-	1	1.44	-	1	3.28	-	1	5.26	-	1

5

The Maybelle River Dune System was found to be advancing into the *Pinus*-lichen community along the eastern edge at a mean rate of 61 cm.yr^{-1} between August 22, 1978 and August 4, 1979 (Table 11). For this time period, maximal advancement was 157.8 cm.yr^{-1} at the most southeastern corner of the dune system. The minimal advancement measured was 5.3 cm.yr^{-1}.

Soil water content tended to be greater under *Hudsonia*-lichen communities compared with *Hudsonia*-sand communities. (Fig. 6). However, when rainfall was infrequent and reduced in amount (Fig. 6, July 1 to 16) the difference was reduced. At the end of this dry period, soil water content under *Hudsonia*-sand communities was greater than under *Hudsonia*-lichen communities at the Dune site.

Recent History

The Blowout and surrounding area has had a recent fire history (Table 12 and Fig. 2). Major fires swept through the area in 1849, 1901, and 1939. Several more localized fires occurred in the years 1873, 1918, 1926, 1931, and 1951 (fire scars on living trees). Based upon tree age it is also probable that fires occurred in the years 1837 and 1892. The oldest living *Pinus* that was sampled was 140 yr in 1977. This tree was located in the northeast corner of the Blowout at the Blowout's greatest elevation. Two trees located in mid-Blowout which probably originated since the Blowout began, were 33 and 38 yr old.

Table 12. Approximate fire dates, and tree ages for the Blowout site. Age is in 1978. See Fig. 2 for location of trees. Tree ages were approximate in some cases; actually 0-3 years older (*), 3-5 years older (**) and 5 years older (***).

Tree	Date of origin	Fire year 1	Fire year 2	Fire year 3	Age in 1978
F1	1940	1962	-	-	38*
F2	1906	1915	-	-	72*
F3	1942	-	-	-	36**
F4	1927	1926	1951	-	51**
F5	1918	1937	-	-	60*
F6	1904	1929	1951	-	74**
F7	1919	-	-	-	59**
F8	1893	1939	-	-	85*
F9	1906	1939	-	-	72*
F10	1837	1849	1931	-	141*
F11	1938	-	-	-	40
F12	1933	-	-	-	55
F13	1945	-	-	-	33*
F14	1850	1873	1901	1932	128*
F15	1895	1926	1940	-	83*

The Pinus-lichen community along the western edge of the Maybelle River Dune System has had a recent fire history (Fig. 7). At the southern end, localized fires have occurred in 1907, 1946, 1959 and 1962. At the mid-section, fires have occurred in 1934, 1939, 1943, 1953 and 1961. The extent of these fires was not determined but indicates a frequent fire occurrence. A complete sampling was not performed and additional fires may have occurred. Tree age increased with distance from open sand into the Pinus-lichen community. The oldest tree measured was 107 years old and the youngest 17 years old. A more extensive sampling of Pinus at the mid-section indicated a lack of very young trees and uneven ages for existing trees. The first group of trees was located at 80 to 90 m from open sand and was 20.2 ± 4.30 yr. The relation between tree age and diameter at 1.3 m height for this group of trees was significant at the 99% level with approximately 50% of the variation in diameter accounted for by age. The relation between tree age and diameter was not well defined when groups of trees were compared at greater distances from the open sand.

DISCUSSION

A complete micrometeorological description is not available for the Blowout and Dune sites. For this reason, NORMS from Fort Chipewyan and Embarass (Longley and Janz, 1978), and a detailed study by Hage and Labine (Bliss and Mayo, 1980) of a steep southwest-facing slope at Richardson Fire Tower were used to describe the study area. The regional climate is cold temperate.There is a potential for frost

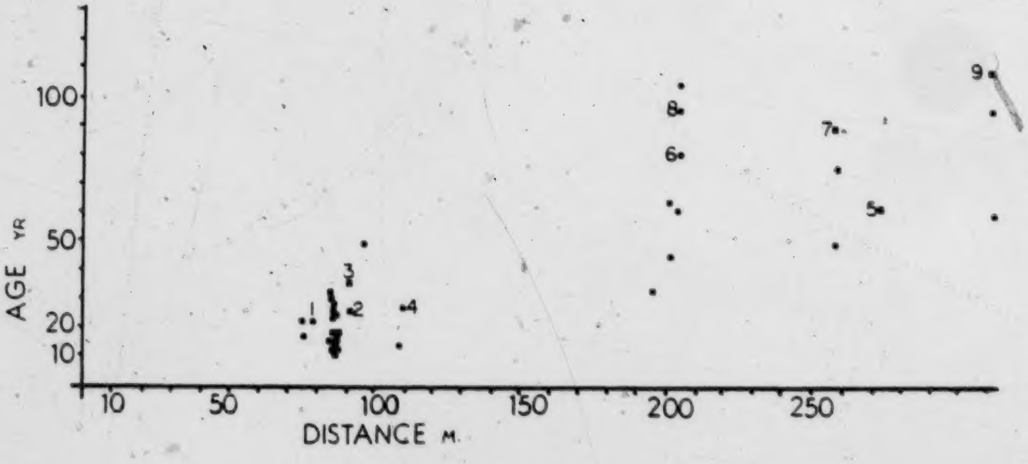

Figure 7 Tree age and approximate fire dates at the Dune site. Trees aged in 1978. Fire dates are #1 = 1962, #2 = 1961, #3 = 1953, #4 = 1959, #5 = 1931, #6 = 1946, #7 = 1939, #8 = 1907 and #9 = 1943; for the southern (●) and mid-dune (■) transects. At 85 and 95 m mid-dune transect, tree age = 11.86 +1.90 multiplied by stem diameter at 1.3 m, $r_{xy} = 0.72$, n=14. Regression of tree age and distance indicates that tree age = -3.14 + 0.321 multiplied by distance from open dune, $r_{xy} = 0.866$, n=34.

at anytime, approximately 1000 to 1200 annual degree d (5°C base), a moderate to low wind speed predominantly from the northwest with some seasonal variation, a high frequency of low intensity precipitation with a few cloud bursts, and, a total annual precipitation of 370 mm. In addition, Hage and Labine (Bliss and Mayo, 1980) report: low wind speeds of 1.5 to 2.0 $m.s^{-1}$ from May to August, seasonal variation in total incoming radiation and net radiation with maximum mean daily values of 300-330 $W.m^{-2}$ and 207 $W.m^{-2}$ in mid-June respectively, air temperatures permanently above freezing by April 5 and snowmelt complete by April 15 in 1977, and, a mean summer precipitation intensity of 10.5 $mm.h^{-1}$. Soil heat flux at Richardson Fire Tower was 7% of net radiation with a net outflow in spring followed by a positive heat flux at snowmelt for the rest of the summer.

Although suitable for generalizations, a detailed extrapolation of NORMS for the study area (Longley and Janz, 1978) or of Richardson Fire Tower micrometeorology (Monthly Record of Meteotological Observations, and, Hage and Labine in Bliss and Mayo, 1980) can only be done with caution. For example, the study sites experienced greater mean daily wind speeds in 1977, four more frosts in 1977, and greater numbers of days with precipitation in 1978 than did Richardson Fire Tower.

Significant deviations from NORMS took place in the period May to August inclusive for the study years 1976 to 1979. It was hotter and wetter largely due to a hot May and a generally wetter summer in 1976, and slightly warmer and wetter due to a hot and wet May and cold

August in 1977. It was slightly cooler and slightly drier due to moderate temperature and precipitation deviation in 1978 and was hotter and drier due to a hot July and a dry May and June in 1979.

The two Blowout sites were located on the same paleo-dune ridge top with similar aspects approximately 100 m apart. As expected, several micrometeorological measures were similar between these sites (Table 4). Although the combined 1977-1978 daily mean air temperatures were not significantly different, the sand community has a smaller amplitude of daily air temperature fluctuation (lower daily maxima and higher daily minima) than the lichen community (Table 5). This occurred despite the greater total daily radiation received at the sand community (Table 5). The moderating infuence of greater wind speeds in the sand community and greater light reflection from white sands account, in part, for the difference in daily maxima and minima. The greater daily mean temperature in the _Pinus_-lichen community versus the _Hudsonia_-sand community along the western edge of the Maybelle River Dune System is similarly explained.

Although plant canopies were open, the presence of _Hudsonia_ standing dead (approximately 10 cm above the ground) was sufficient to shade the soil and reduce soil temperature compared with _Hudsonia_ without standing dead (1 cm above the ground) (Table 6).

Air and soil temperatures in the _Hudsonia_-sand community were greatest at the soil surface during the day and greatest at approximately 10 cm in the soil at night (Fig. 3). Hage and Labine (Bliss and Mayo, 1980) report soil heat flux of 7% of net radiation under a 20 yr old Pinus-lichen covered slope. A significantly greater soil heat flux could be expected for the Blowout.

Soils in the Blowout are Orthic Regisols. Under existing and previously vegetated Pinus-lichen communities, Eutric and Eluviated Eutric Brunisols were found (Fig. 5). Their profiles were obscured by sand deflation and evidence of past fires.

The soils of Pinus-lichen communities, Hudsonia-sand communities and open sand areas were very nutrient poor and did not contain significant amounts of silt or clay (Table 9). No significant differences with depth or between sites were detected, possibly due to the relatively 'crude' analyses which were designed for agricultural applications.

In the 1978 field season, soil water contents (0-30 cm) only dropped below 5.0% (dry wt.) after an extended period without precipitation or only very low intensity precipitation (Fig. 6). During this period, the difference between soil water content under the Hudsonia-lichen community and the Hudsonia-sand community decreased until soil water content was greater under the Hudsonia-sand community (Fig. 6). As the lichen mat has a high resistance to water loss at low water contents it acts as an effective barrier to water loss from the underlying soil (Lindsay in Bliss and Mayo, 1980 and Larson and Kershaw, 1976). However, during extended dry periods, the lichen mat can intercept precipitation and retain approximately 1.8 $mm.hr^{-1}$ before significant infiltration occurs (Lindsay, in Bliss and Mayo 1980). If only low intensity precipitation occurs continual drying of the underlying soil would occur, whereas the open sands would be partially rehydrated. It is probable then, that more severe droughts can develop under the lichen mat and that the soil water conditions are generally more moist under this mat than under open sand.

Detailed analysis by MaClean (Bliss and Mayo, 1980) indicate that these soils have a low water holding capacity. Between field capacity (-0.006 MPa) and 'permanent wilting' (-1.5 MPa), only 58-95 mm of water per m of sand is available to the plants. Extremely high saturated hydraulic conductivities (approximately 30 to 57 $cm.hr^{-1}$) account for estimates of 48% precipitation loss through drainage. Despite these soil properties, MaClean (Bliss and Mayo, 1980) conclude that *Pinus* did not suffer plant water stress during the 1977 field season at Richardson Fire Tower. The high frequency of rainfall, high resistance of the lichen mat to water loss and *Pinus* response to vapor pressure deficit support this conclusion.

The Blowout experienced relatively low wind speeds with occasional high speed gusts. The most exceptional day was August 9, 1977 with speeds at $120km.hr^{-1}$. Rates of sand deflation and deposition were noted to vary according to wind speed and direction, soil moisture level, and local microtopography. Based upon sand deposition and deflation patterns, it appears that the time periods without snow cover before and after the field season were as significant as the summer months for sand movement (Table 10). Rates of sand deposition within the Blowout approximate the rate of sand deposition at the Blowout perimeter. Sands at both study sites, the Blowout and the

Dune, are actively burying the neighboring Pinus-lichen woodland (150 mm.yr^{-1} and 610 mm.yr^{-1}, respectively). Both study sites experience cyclic patterns in sand deflation and deposition, and in hummock or ridge building and erosion. The presence of Hudsonia or grass species such as Agropyron have significant affects on sand movements (Table 10 and 11). Ridges or hummocks within the study sites were always associated with their presence and bowls or hollows with their absence.

A high frequency of fires at the study sites is suggested from the tree fire scar and tree age data (Table 12 and Fig. 7). Fire evidence in soils (Fig. 5) suggests that the Blowout originated from a fire disturbance and grew to its present size as a result of wind erosion. The presence of depositional slopes along the Blowout perimeter further suggest that the paleo-dune crest is actively being blown out towards the eastern perimeter.

The Dune Field study site origin is likely to have resulted from fire disturbance and can be traced back to the Athabasca River. The orientation and extent of dunes within the Dune Field is strongly influenced by wind patterns, local topography and plant colonization influences.

STUDY SITE: PLANT SYNECOLOGY

INTRODUCTION

The vegetation of the study area has not been intensively studied. Rowe (1972) defines the area as part of the Athabasca South section of the Boreal Forest. Open park-like P. banksiana-lichen woodlands occupy upland drier sites and are floristically simple. Approximately 60 vascular plant species have been found throughout the area (Raup and Argus, 1982) however, any one location is often much more species poor. For example, 60% of sites with Pinus had 5 or less vascular plants in a survey of Pinus-lichen woodlands in northeastern Alberta and northern Saskatchewan (Carroll and Bliss, 1982). More mesophytic forests found on floodplains consist primarily of P. banksiana, Picea mariana, Picea glauca and Betula papyrifera. Low-lying wetlands consist of P. mariana/Larix larcinia muskegs. Raup and Argus (1982) have recently summarized vegetation studies on aeolian landforms in this area; Williams River sand dunes (Hermesh 1972); Lake Athabasca sand dunes (Rowe and Hermesh 1974); and, the Maybelle River Dune System (Landals, 1978 and Nielson 1978). They point out the botanical uniqueness of these areas; a collection of plants derived from arctic, boreal, and Great Plains elements, great variation in total species between dunes, and, a high degree of endemism. For example, the Williams River dunes contain 10 endemics in a total of 27 vascular plants, whereas, the Maybelle River dunes have 1 endemic in a total of 9 and generally lack the arctic element (Raup and Argus, 1982).

Successional patterns in the area have not been fully investigated. Several authors have drawn attention to the importance of fire in determining vegetation patterns in the Boreal Forest (Scotter 1964, Rowe and Scotter 1973, Kershaw and Rouse 1976, Maikawa and Kershaw 1976, Cayford and McRae 1981, Johnson and Rowe 1977, and Black and Bliss 1979. Carroll and Bliss (1982), conclude that fire history is the major determining force in vegetation patterning in the study area. They considered three phases of plant succession after fire: recolonization and reestablishment mainly by *P. banksiana* seed germination and other early lichen, moss and vascular plant colonizers (*Cladonia coccifera*, *C. gracilis*, *Polytrichum piliferum*, *P. juniperum*, *H. tomentosa*, *Carex foenia*, *Agrostis scabra* and *Epilobium angustifolium*); vegetation recovery in which the most significant floristic change is the replacement of *C. gracilis* and *C. coccifera* by *Cladina mitis*; and if not disturbed by fire, canopy closure by *P. mariana* and expansion of *Cladina stellaris*, *Cladina rangiferiana*, *Pluerozium schreberi*, *Dicranum polysetum* and *Ptilidium ciliane* in specialized mesic sites. A mean fire return interval of 40.4 yr was calculated for these *Pinus*-lichen woodlands (Carroll and Bliss, 1982), precluding the third phase in most cases.

The vegetation of sand dune areas has been categorized by Raup and Argus (1982). They recognize several vegetation patterns or plant assemblages associated with hillock and cushion dunes, rolling dune topography, transverse dunes, oblique ridge dunes, parabolic dunes, gravel pavements, and dune slacks. Raup and Angus (1982) and Landals

(1978) refer to the involvement of P. piliferum and Hudsonia in the revegetation of the windward margin of large parabolic dunes. However, Raup and Argus (1982) conclude that it is not appropriate to describe succession in dune areas simply based on spatial arrangements of plant assemblages. As noted by other authors (Olson, 1958, and Ranwell, 1972) succession appears to be multidirectional as determined by the influence of the many possible combinations of independent variables.

In this section the vegetation of the study sites will be described and the role of Hudsonia in revegetation and succession discussed.

MATERIALS AND METHODS

Field observations on vegetation within the study area were made at both study sites and on areas between Richardson Fire Tower and the Blowout. Extensive plant collections were not made throughout the study area, but were limited to the Blowout study site and the Dune site. Field observations were not made at the large dune fields on the south shore of Lake Athabasca due to logistic problems.

Transects were run at both study sites. At the Dune site, two transects were intensively analyzed from open dune flat into the revegetating flat plain of Pinus-lichen woodland along the western edge of the dune field. One was run in the southern portion of the dune field parallel to the southern most leading edge of the dune field, and one at the mid-dune field position, approximately perpendicular to the nearest large transverse dune ridge (Plate 4). The exact position of each transect was chosen to avoid excessive secondary blowouts so that as much as possible spatial change in plant assemblages represented temporal and, therefore, successional sequences in plant assemblages. At 5 m intervals, species, their cover, and numbers were recorded in 1 m^2 plots. The number of *Pinus* was recorded in 25 m^2 plots. Several less intensive transects were also run to varify the representativeness of the intensive transects.

An intensive transect was run across the Blowout into the *Pinus*-lichen woodland. Based on plant growth form, and sand deposition and deflational characteristics, *Hudsonia* site types were defined within the Blowout and Dune sites.

Nomenclature for vascular plants, bryophytes, and lichens follows Moss (1959), Crum (1976) and Hale (1969) respectively.

RESULTS

A limited number of vascular and non-vascular plants was found at the Blowout (Table 13) and along transects from the open sand into the revegetated western edge of the Maybelle River Dune System (Fig. 8). Species composition and cover were found to vary with distance from the open dune. *Hudsonia* was the first vascular plant ~~to~~ achieve dominance (Fig. 8) and formed a large *Hudsonia*-sand zone without significant presence of other species. It was the only vascular plant which maintained importance along the entire transect. In the northern part of the dune system and in the mid-dune field transect,

Table 13. Important species and site characteristics for the Blowout. Hudsonia growth form was categorized as vegetative (VEG - mostly current year growth) and as standing dead (SD - mostly two or more years old). The number of Hudsonia twigs transversing the sand surface was either low (L), medium (M) or high (H) and the amount of branching per twig was either sparse (S), intermediate (I) or dense (D). Sand movement was measured from August 1977 to August 1979. Cover values for species, litter and bare sand were rated as either present (P), less than 10% (0), 10 to 30% (1), 30 to 50% (2), 50 to 70% (3), 70 to 90% (4) and 100% (5).

	P. banksiana lichen woodland flats		Border ridge			Sand communities within the Blowout			
	Between border ridge, NE side of Blowout	SW side of border ridge	Top of ridge	NE slope	SE slope	Strongly depositional slope	Depositional sand plateau	Deflational sand plateau	*Polytrichum piliferum* plateau
TREE LAYER									
Stem density (ha^{-1})	1200	1600	varied		0	0	0	0	0
HUDSONIA TOMENTOSA									
Growth form	-	SD+VEG.	SD+VEG.	VEG.	SD+VEG.	VEG>VEG SD+VEG	VEG+SD	SD+VEG	SD+VEG
Density of branches per twig	-	S	S	S	S	D	S	I	I
Sand movement (mm.yr^{-1})	0.0	0.0	0.0	38.8	0.0	33.1	3.5-16.8	-0.2	0.0
Number of twigs transversing sand surface	-	L	L	L	L	H	H	L	L
Cover	-	P	P	1	P	3	3	2	1
SHRUB LAYER									
Alnus crispa		P							
Ledum groenlandicum		P							
Pinus banksiana	P	P	P	P			P		
Populus tremuloides	P		P						
Prunus pensylvanica	P								
GROUND LAYER									
Lichens									
Cetraria ericetorum			P		P				
C. nivalis	P	P	P				P		P
Cladina mitis	3	3	P		1		P		P
C. rangiferina		P							
C. stellaris		P	P						
Caldonia amaurocraea		P	P						
C. bellidiflora			P		P				
C. gracilis	P	P	P		P				P
C. phyllophora		P	P		P				P
C. uncialis			P						
C. verticillata		P	P		P				
Stereocaulon tomentosa		P	P		P				
BYROPHYTA									
Polytrichum juniperinum	P	P					P		2
P. piliferum	P	P	P		2				
Pleurozium schreberi	P	P							
Dicranum polysetum	P								
D. undulatum	P	P							
Ptilidium ciliare	P	P							
VASCULAR PLANTS									
Grass sp.		P							
Agropyron smithii			P				P		
Carex foenea			P						
Arctostaphylos uva-ursi	P	P	P	P					
Artemisia campestris			P				P		
Cornus canadensis		P							
Mianthemum canadense		P	P						
Potentilla tridentata			P				P		
Solidago sp.							P		
S. decumbens			P		P		P		
Stellaria longipes			P				P		
Vaccinium myrtilloides	P	P							
V. vitis-idaea	P	P							
LITTER									
Pinus banksiana	2	2	P	P			P		
BARE SAND			P	6	2	2	2	3	2

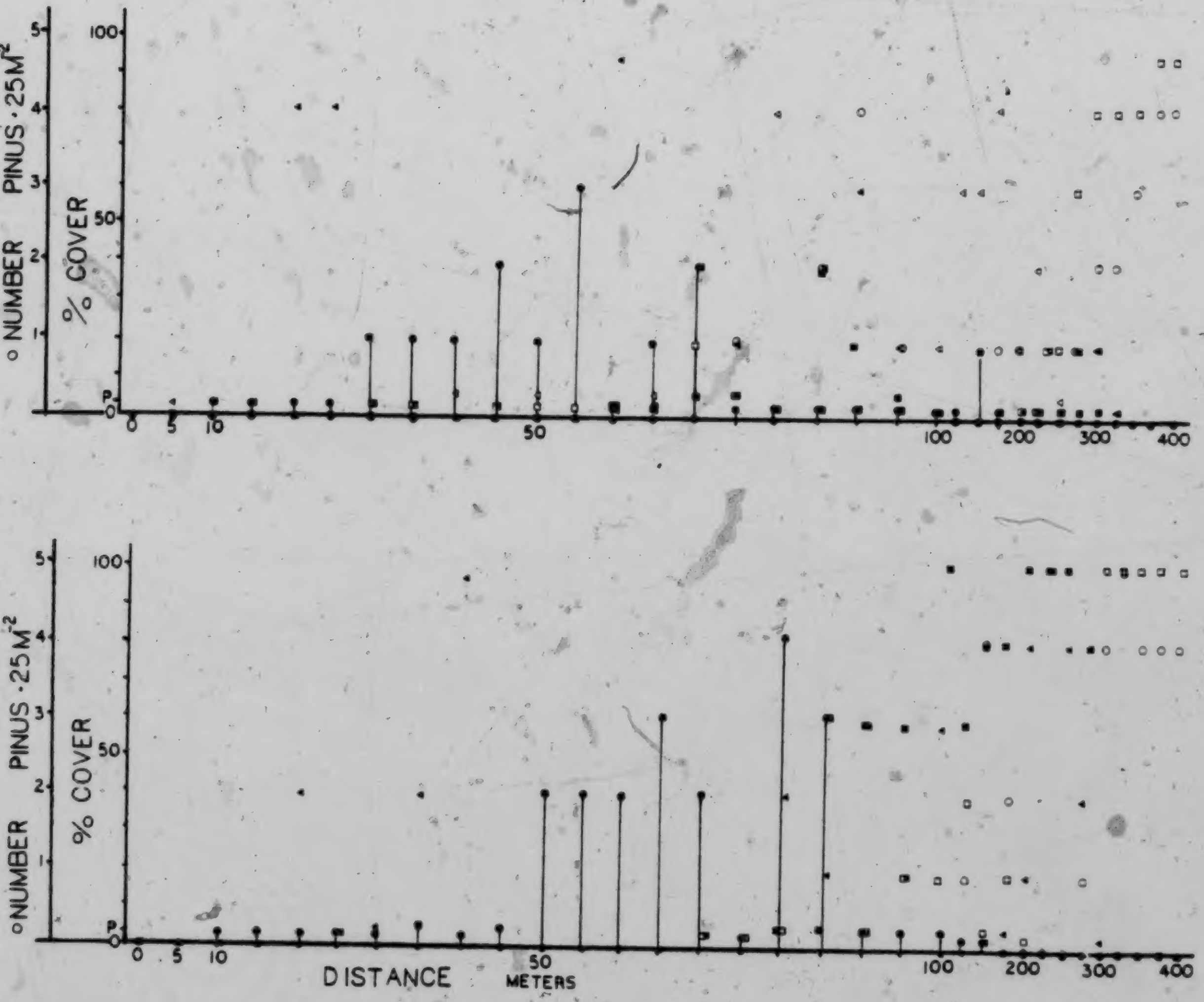

Figure 8 Percent cover for the main species along transects from open dune field to revegetated Pinus banksiana-lichen woodland, western edge of the Maybelle River Dune Field. Data represents percent cover within a m^2 or number of P. banksiana (○) per 25 m^2 sampled August, 1978. The main species of the south transect (A) and the mid-dune field transect (B) were: Hudsonia tomentosa (●), Empetrum nigrum (◁), Polytrichum piliferum (◀), upright Cladina and Cladonia type lichens (□), and 'crustose' type lichens (■).

E. nigrum assumed an increasing significance, especially in areas of moderate to low sand deposition (Fig. 8 and Plate 5), however, Hudsonia was able to withstand a much greater degree of sand deposition then E. nigrum. Sand deposition in the Hudsonia-sand zone resulted in shallow dune building (Plate 5). In more protected areas, a hummock and hollow topography with larger mats of Hudsonia occurred. This zone was often preceded by a zone of P. piliferium (Plate 5), which could be extensive and usually consisted of gravel pavement intermixed with the occasional Hudsonia plant. Sand deposition in these areas was mostly centered around isolated Hudsonia plants and was not extensive (Fig. 9).

The Hudsonia-sand zone was followed by a gravel pavement zone characterized by; decreasing number and vigor of Hudsonia, high levels of P. piliferum and increasing levels of fruticose Cladina/Cladonia lichens, and 'crustose' type lichens including high levels of primary squamules of C. bellidiflora (Fig. 8 and Plate 5B, C and D). Sand deposition was negligible (Fig. 9), and Hudsonia persisted throughout this zone. However, a decline in Hudsonia cover coincided with an increase in lichen cover throughout this zone (Fig. 8) and a decrease in the amount of net annual production per amount of previous years' growth (Fig. 9). A secondary disturbance, causing sand deposition, resulted in an increase of Hudsonia cover, biomass and amount of net annual production per amount of previous years' growth (Figs. 8 and 9). Initiation of lichenization was associated with Hudsonia. Centers of Cetraria nevalis and most Cladina/Cladonia growth were

Plate 5 Transect from open *Hudsonia*-sand community into the *Pinus*-lichen woodland, western edge of Maybelle River Dune System. Site types are *Hudsonia*-sand community (A), *Hudsonia*/*Polytrichum piliferum*/gravel pavement (B), *Hudsonia*/*P. piliferum*/lichen/gravel pavement (C and D), *Pinus*-lichen woodland (E) and open bowl in *Pinus*-lichen woodland (F).

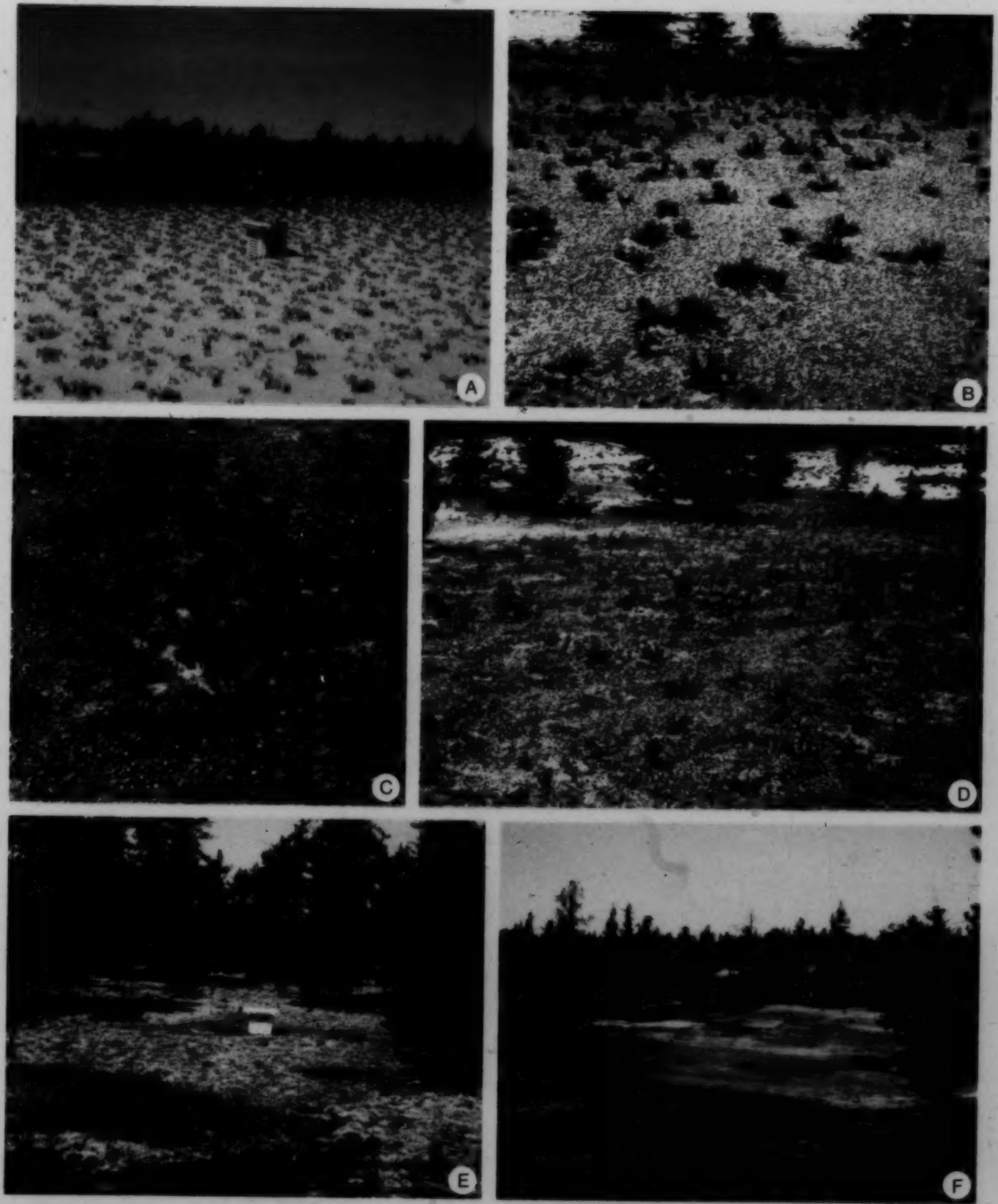

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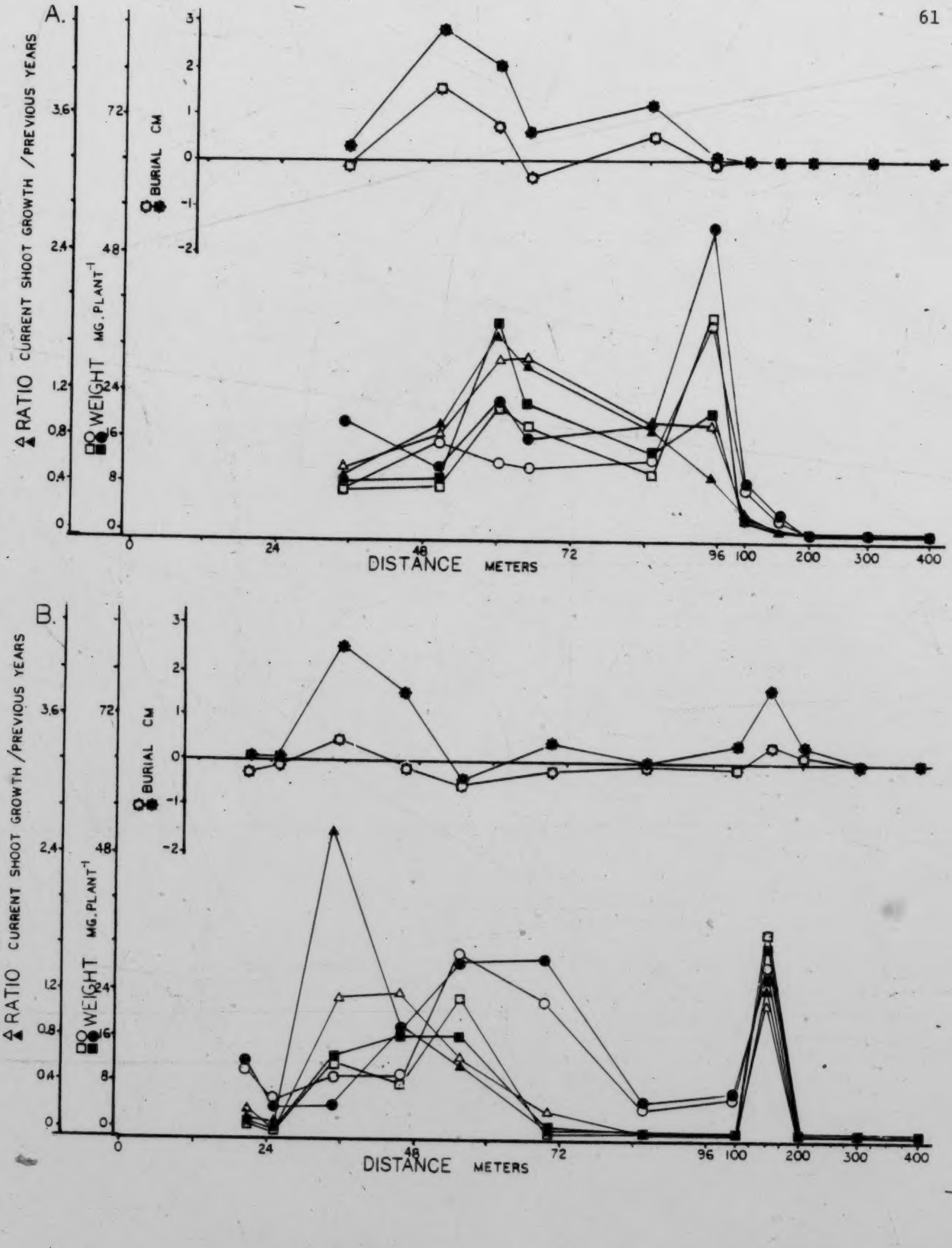
Figure 9 Hudsonia dry matter allocation along transects from open dune field to revegetated Pinus-lichen woodland, western edge of the Maybelle River Dune Field. Solid symbols are for August 7, 1979 and open symbols are for August 22, 1978. The amount of sand burial in 1978 (✪) was determined from original measures in late May 1978, and, since the August 1978 reading for 1979 (✹). Ratio of net annual production (□ , ■) to previous years' growth standing aboveground (○ , ●) are indicated by △ and ▲ for the south transect (A) and the mid-dune field transect (B) on a per plant basis.


A.
△ ▲ RATIO CURRENT SHOOT GROWTH / PREVIOUS YEARS
□ ■ ○ ● WEIGHT MG. PLANT^{-1}
○ ● BURIAL CM
3.6
2.4
1.2
0.8
0.4
0
72
48
24
16
8
0
3
2
1
0
-1
-2
0
24
48
72
96
100
200
300
400
DISTANCE METERS
B.
△ ▲ RATIO CURRENT SHOOT GROWTH / PREVIOUS YEARS
□ ■ ○ ● WEIGHT MG. PLANT^{-1}
○ ● BURIAL CM
3.6
2.4
1.2
0.8
0.4
0
72
48
24
16
8
0
3
2
1
0
-1
-2
0
24
48
72
96
100
200
300
400
DISTANCE METERS

determined by attachment of wind blown fragments onto Hudsonia (Plate 5B, C and D). Other lichen species became more prominent as distance from the open dune increased within this zone, unless a secondary disturbance occurred. Few scattered Pinus of varying ages and sizes were found in this zone. The transition from this zone into the Pinus lichen woodland (Plate 5E) was often very abrupt and at least partially disturbed. Complete Cladina/Cladonia lichen mat and tree canopy closure were not common along these transects (Plate 5E). Both were far more common on the eastern edge of the Maybelle River Dune System and other more mesic Pinus-lichen woodlands. The revegetated Pinus-lichen woodland was extremely dry and was intermixed with large stabilized bowls of gravel pavement, P. piliferum, few scattered Hudsonia and 'crustose' type lichens especially C. bellidiflora squamules (Plate 5E).

Photo observations (Plate 6) and ground surveys indicated that the two intensively studied transects were not representative in terms of the degree of secondary disturbance. A higher degree of disturbance (especially due to blowouts) in the pattern of species change with distance from the open dune was more characteristic.

At the Blowout, the surrounding Pinus-lichen woodland flats were more species rich than the Blowout itself, a total of 27 versus 12 species (Table 13). In terms of cover the important species in the Pinus-lichen woodland surrounding the Blowout included Vaccinium myrtilloides, C. mitis and P. banksiana. The only species of importance in the Blowout was Hudsonia. Within the Blowout, areas of

Plate 6 Western edge of the Maybelle River Dune System showing secondary disturbance of the vegetation sequence.

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high sand deposition had greater numbers of Hudsonia plants and cover. Low cover and less numbers were associated with P. piliferum sand communities (Table 13).

Hudsonia was also observed to be an earlier colonizer of burn sites in the study area (Plate 7).

DISCUSSION

Pinus communities recognized at the study sites are similar to those described by Carroll and Bliss (1982). However, in the study area, the P. banksiana/V. myrtilloides/C. mitis community was more restricted to low lying moist areas or shore lines. The more xeric, P. banksiana/C. mitis community dominates in much of the study area on upland sites. The revegetated woodland on the western edge of the Maybelle River Dune System and the vegetation of border ridge tops at the Blowout represent a more xeric form of this community type. Canopy and lichen mat closure are unlikely to occur at these sites due to xeric conditions and exposure to a high frequency of wind and fire disturbances. Pinus exhibited a stunted growth form in these habitats and was often heavily infected by Arceuthobium americanum. The lichen mat in both sites formed hummocks approximately 10 to 20 cm in diameter due to wet-swelling; dry-shrinking cycles. This lichen hummock habit prevented lichen mat closure, exposed bare sand around the hummock edge, and allowed for easy displacement of the hummock.

The only vascular plants to achieve any significance in these most xeric P. banksiana/C. mitis sites were Pinus and Hudsonia. Studies by Raup and Argus (1982) indicate that E. nigrum can assume significance

Plate 7 Extent of Hudsonia growth and sequence of flower opening in a recent (7 yr) burn site.

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in similar sites on the southern shore of Lake Athabasca. P. piliferum and the Cladina/Cladonia lichens were almost always present.

The species and pattern of vegetation change from open dune to revegetated P. banksiana/C. mitis woodland along the western edge of the Maybelle River Dune System differs from that described by Carroll and Bliss (1982) for revegetation of forested areas after fire. For example, a distinct phase of Hudsonia and P. piliferum as primary colonizers precedes any lichenization phase. The process of lichenization is much slower and not evident until Hudsonia forms an upright growth form with a considerable amount of standing dead. The area subsequently becomes protected from high-winds and sand deposition or deflation. In this regard, the dune building ability of Hudsonia may play a significant role in altering wind patterns allowing for successful lichenization and Pinus invasion. Also, the species involved and the method of invasion vary. For example, Hudsonia is the only vascular plant of significance, invading the area by seed (Plate 5A). And, early lichenization involves C. nevalis and not just Cladina/Cladonia lichens as found in disturbed forest areas. Also, initial lichen invasion is mainly by wind blown fragments attaching to Hudsonia.

The time period for revegetation at the Blowout and Maybelle River Dune System is difficult to determine. However, Landals (1978) indicated a rate of plant advance into the Maybelle River Dune System of approximately at 1-1.5 $m.yr^{-1}$ based on variation in tree age along transects from open dune into the invading forest. Data presented here indicate a rate of 2.3 $m.yr^{-1}$ (Fig. 7). At both sites there were considerable interruptions in vegetation patterns. This was due to cyclical and varied patterns of sand deflation and deposition, dune building and erosion, and, altering wind patterns. The resulting complexity of vegetation patterns precludes a simple determination of successional change based on the spatial arrangement of plants. However, the following sequence of events and vegetation change for revegetation of open sand on the western edge of the Maybelle River Dune System is suggested: the establishment of a *Hudsonia*-sand community either by seeding into an existing *P. piliferum* sand zone or invasion into open sand; *Hudsonia* dune building resulting in protection of older *Hudsonia* stands, lichenization and *Pinus* seed invasion into older protected *Hudsonia* stands; and eventually, progress towards lichen and tree canopy closure. If lichenization and *Pinus* seed invasion are limited, large open stabilized bowls of *P. piliferum* occur. It is likely that a moderate amount of sand deposition is required for *Pinus* invasion. Disturbances resulted in small blowouts and secondary *Hudsonia* dune building if a supply of sand was available. Seeding-in of *Pinus* appears to be highly variable and is mostly restricted from the open *Hudsonia*-sand communities. Due to secondary disturbances, islands of *Pinus* become isolated and older trees are found in *Hudsonia*-sand communities.

The decline of *Hudsonia* vigor with lichenization is quite apparent (Plate 5, Figs. 8 and 9). Lichen removal experiments, and field observations indicate that this decline may be related to aging and to the presence of lichens. The development of excessive soil drought under the lichen carpet, elevated leaf temperatures and the potential for allelopathic leachates from Cladina/Cladonia lichen (Brown 1967, Brown and Mikola 1974) may explain this decrease in Hudsonia vigor.

Hudsonia was found throughout the study areas on stabilized and unstabilized aeolian landforms. It was most prominent in the apparently more xeric sites and was of decreasing or no importance in mesophytic Pinus-lichen woodlands and wetland sites. Hudsonia was the most prominent vascular plant on the open sands of the windward margin of parabolic dunes, and in border ridge blowouts. It was also common on interdune flats successfully growing in gravel pavement, on the leeside of large transverse dune crests, roadsides, and burn sites.

Several Hudsonia community types have been defined from these plant community and site studies. They include: Hudsonia-strongly depositional sand community, Hudsonia-slightly depositional sand community, Hudsonia-deflational sand community, Hudsonia/P. piliferum community and Hudsonia-lichen community. Several of these are floristically similar, however, they vary in Hudsonia growth form and vigor.

AUTECOLOGICAL INVESTIGATIONS

INTRODUCTION

Autecological data on the genus Hudsonia are limited. Morse (1979) has compiled the most complete systematic and ecological biogeographic study of the genus. He concludes that within the genus, H. tomentosa colonizes the most xerophytic sand sites and has the greatest number of xerophytic and psammophytic adaptations.

Psammophytic adaptations, noted mainly by Morse (1979) and also by Hall (1956) and Skog and Nickerson (1972) include: prevention of physical damage from windblown sand by triangular tightly imbricated leaves with a heavy complete pubescence, highly reflective pubescence for reduction of leaf temperatures, ability to withstand slow moderate sand burial and adventiously root into sand, an apogamous breeding system apparently not necessarily relying on insect visitations, and a variety of xerophytic adaptations. Similarly, Hermesh (1972), Landals (1978), Nielsen (1978), and Raup and Argus (1982) have noted the ability of Hudsonia to withstand slow, moderate sand burial. Morse (1979) notes several well known xerophytic adaptations relating to survival in droughty habitats. These include: a shallow fibrous root system with the occasional deep root, small densely pubescent appressed leaves, small ephemeral flowers, and a tightly enclosed developing fruit. Hall (1959), Skog and Nickerson (1972) and Morse (1979) note that Hudsonia, especially H. tomentosa, is unable to withstand shading.

In terms of ability to colonize sand areas, Morse (1979) noted Hudsonia establishment was most consistently by the vegetative clone-forming habit. Seeds remain viable for several years: Morse (1979) successfully germinated 1 of 2 herbarium samples dated from 1913. Seeds germinate in large numbers under suitable conditions, however, seedling mortality rates are high.

The objective of this section is to determine autecological characteristics of H. tomentosa which relate to its ability to colonize and thrive on the open sand dunes and blowouts in northeastern Alberta. These will include phenologic observations, and measures of plant biomass, productivity, carbon allocation strategy, and seed germination. As the thesis of Morse (1979) was not available when these studies were planned and carried out (1976-1979), it is only in retrospect that a detailed comparison between H. tomentosa in northeastern Alberta and Morse's study area can be made.

MATERIALS AND METHODS

The clone-forming habit of Hudsonia in many cases prevented the clear distinction between isolated individuals, especially in areas experiencing sand deposition. A mature plant was, therefore, visualized as consisting of one to several individual twigs transversing the soil-air interface. Unless otherwise stated, observations and measurements were made on individual twigs. In the text they are referred to as plants. These plants were randomly selected within certain site types and clearly marked in 1977 at the Blowout site and in 1978 at the Dune site.

Phenology

Phenologic events were studied at the Blowout site in 1977 and 1978, and at the Dune site in 1978. Less detailed observations were made at Richardson Fire Tower runway in 1976 and at both the Blowout and Dune sites in 1979. The following phenophases described by Flint (1974) were studied: seed germination, seedling growth, vegetative shoot growth, flowering and fruiting, and fall dormancy. Phenologic patterns were compared to degree-days (5°C threshold) and total precipitation as measured at Richardson Fire Tower from April 23 and 24 of 1977 and 1978, respectively.

Production and carbon allocation strategy

Aboveground biomass, net production and allocation of carbon to vegetative and reproductive tissue were measured on a 1 m^2 or per plant basis in 1977 and 1978. These observations were made on several different Hudsonia site types at the Blowout and Dune sites.

At the Blowout site in 1977, 14 plants were clearly marked per Hudsonia site type. Subsequent plant disappearance, loss of marker or misplacement of marker reduced this number and precluded the use of certain site types in certain analyses. At the Dune site, three plants were marked per sand movement measurement station. Individual plants were sequentially measured from the sand surface up. The measures were recorded so that individual measurements could be compared from one date to the next. Length measurements were made on standing dead, last year tissue, current year growth attached to last year tissue, current year growth attached to current year, and length of short shoots supporting reproductive growth (short reproductive shoots). The sum of standing dead and last year growth was referred to as previous years' growth. Last year growth could be distinguished from the green current year tissue and the black to grey standing dead as it was tan to brownish-grey coloured. Reproductive growth was counted and classified as flowers closed (sepals and petals not yet open), flowers open (petals open and attached), flowers finished (petals fallen but fruit still attached to short reproductive shoot) or flowers fallen (fruit had fallen off the plant). Shoots were measured to the nearest 0.025 cm and buds smaller than 0.05 cm were size classed. Length measurements and flower counts were converted to dry weights using regressions derived from samples collected at the time of measurement. The short shoots associated only with reproductive growth were considered as part of the total reproductive growth. In this regard, net annual production measures after fruit fall included fruit weight. In all cases net annual production did not include roots, and the term allocation refers to the percent allocation between vegetative and reproductive shoots unless a specific reference is made to allocation between roots and shoots.

Aboveground net production and biomass were determined at both study sites on a per 1 m^2 basis. Samples at the Dune sites were collected at 5 m intervals along transects from open sand into the Pinus-lichen woodland. At the Blowout site samples were collected within Hudsonia-site types. A 1 m^2 square with six fixed 50 cm^2

sections was used to collect plant tissue. Six m^2 were randomly laid down and a fixed section sampled by collecting plant samples at the sand surface. Samples were heat killed, separated into components and dried for 24 hr at 60°C before weighing.

Sand burial and lichen removal experiments

In order to determine the effect of sand burial on the growth of Hudsonia, experiments were performed at the Blowout site in both 1977 and 1978. Within the various Hudsonia-site types (3 in 1977 and 4 in 1978), similar mature plants were selected and the length of tissue types determined for individual plants. Burial subplots (1 m^2) were established within each Hudsonia-site type and experimental plants were buried to the tip of the highest growth (1978 only), or to a height 1 cm below the highest growth point (1977 and 1978). In 1977, plants were buried for the first time July 24 and plots were not maintained on a regular basis. Dry sand was sprinkled on the burial plots to maintain levels of burial once a week in 1978, starting May 26. Net amount of burial was determined using the glass slide technique and by referencing the sand surface to a fixed point on each twig. The effect of burial on plant performance was monitored on the same plant and compared to controls using techniques described above.

In order to determine the effect of the lichen carpet on growth of Hudsonia, a 5 by 5 m area was cleared within the lichen plot on August 1, 1977. Individual plants were marked and analyzed for tissue lengths. Plants were chosen based on their similarities and position on the slope. Control plants were, at a minimum, 1 m from the edge of the removal area. Wind blown lichen fragments were periodically cleared from the plot.

Seed germination and seedling ecology

From 1977 to 1979, the location and fate of collections of seedlings were followed. In 1978 a transect was run across the Blowout, and along the transect from open dune to Pinus-lichen woodland at the Dune. Seedling age and numbers were recorded such that each seedling could be followed separately.

Seedling root:shoot ratios were determined on samples dried at 60°C for 24 hr. Plants greater than 2 yr could not be accurately aged.

A large collection of fruit was made at the Blowout and Dune sites. These collections were used in seed germination studies. Seeds were separated from the fruit by a combination of the following techniques: rubbing fruits between two slabs of wood covered by sand paper, air blowing of remains to separate the lighter petals and sepals from the seed and vacuuming of good seed to isolate it from degenerate seed. The seed coats had to be air blasted in a chamber lined with sand paper in order to achieve scarification necessary for proper imbibition. Unless otherwise stated, seeds were germinated in petri dishes containing distilled water, at 20°C and constant light.

Germination was tested in relation to various osmotic concentrations. Thirty imbibed seeds were used in treatments of polyethylene glycol (PEG) 6000, at osmotic strengths of 0.0, -0.3, -0.6, -0.9 and

-1.5 MPa. All preparations were kept at 20°C and constant light (75 uE.m^{-2}. sec^{-1} PhAR).

RESULTS

Phenology

Preformed buds of Hudsonia overwintered in a fall-coloured state, orange to brown colour. Following snow-melt these buds broke dormancy greened-up and had begun stem expansion prior to my arrival at the study sites in late May of 1977 and 1978. A cold May delayed this expansion in 1978 (Fig. 10). These preformed buds expanded to an average shoot length of 4 mm during the season. Most of these short reproductive shoots bore one flower and usually degenerated slightly prior to fruit fall. The occasional short reproductive shoot bore vegetative primordia which expanded later in the season. Most flower-bearing shoots were subapical (Fig. 11). Flowers remained open for as little as 1 d but usually persisted for 2-4 d. Night-time petal closure was common. Flower opening occurred sequentially in time from the warmest part of a plant or site to the coolest (Table 14). Branches closest to the soil surface had earliest flower opening. Flower opening occurred over a longer period of time in 1977 than 1978. In 1978, early June was cool and damp and a dramatic flush of flower opening occurred on June 24-30 when air temperatures were considerably warmer. Developing fruits remained on the plant for 30-50 d and were susceptible to fall during high wind periods.

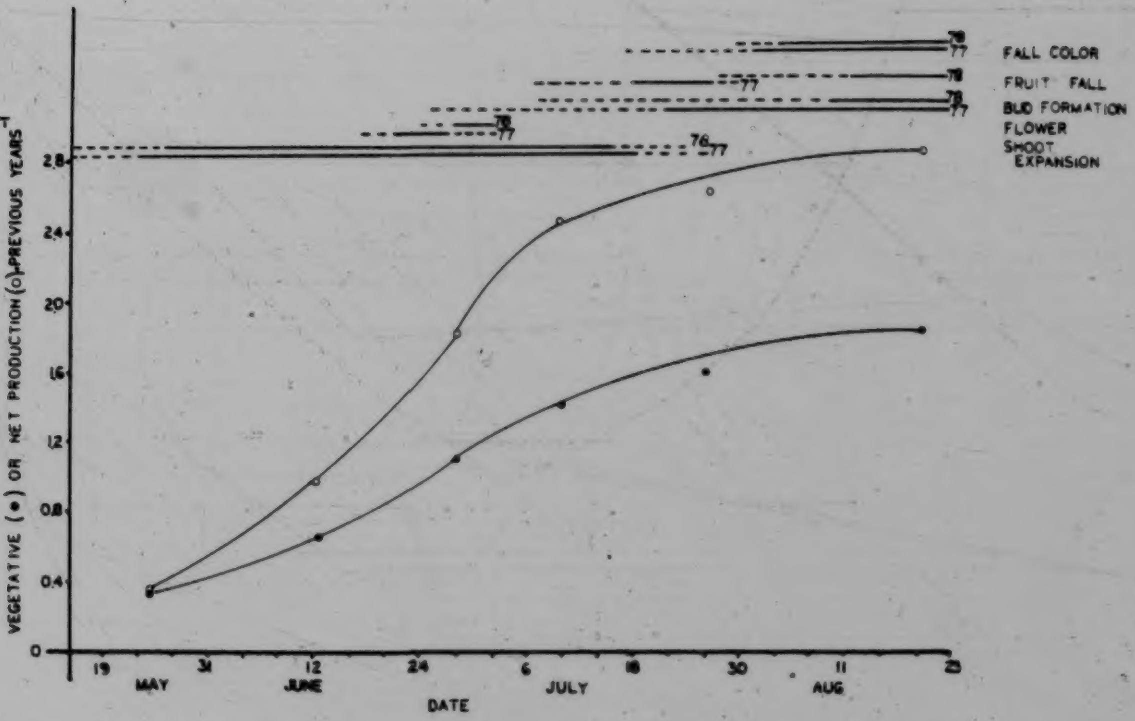


Figure 10 Phenologic events and seasonal change in *Hudsonia* carbon allocation at the Blowout site, 1977 and 1978. The concentrated period for phenologic activity and the preliminary or final stages are indicated by ___ and --- respectively. The amount of vegetative (●) and net production (○) per amount of previous years' growth are indicated for 38 plants.

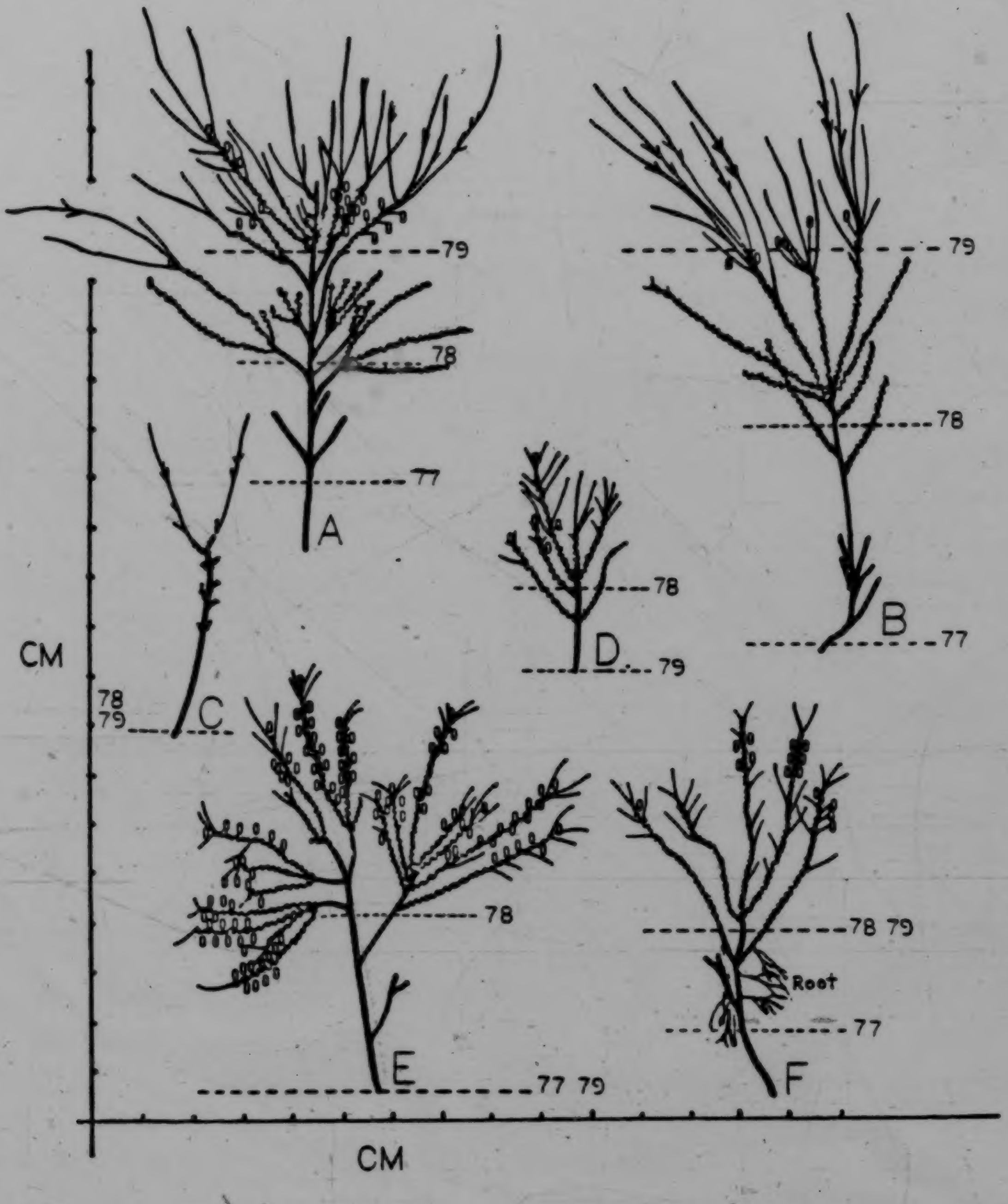


Figure 11 Diagrammatic representation of *Hudsonia* growth response to sand burial and the amount of previous years' growth. Representative plants are diagrammed, A and B = *Hudsonia*-sand community at base of strongly depositional slope, C = *Hudsonia*-sand community without standing dead, D = *Hudsonia*-sand community without standing dead, burial experiment in 1978, E = *Hudsonia*-lichen community, lichen removed 1977, burial experiment in 1978, and, F = *Hudsonia*-lichen community, burial experiment in 1978. Current year vegetative growth (—), current year minus one (〰), current year minus two or more (▬), current year reproductive growth (0) and sand level in 1977, 1978 or 1979 (- - -) are indicated.

Table 14. Influence of temperature on flower opening, Blowout June 25, 1978. Measurements made on 2 plants just prior to the main flush of flower opening at this site, n = 7 for each measure. Significant difference between southeast- and northwest- facing sides of each plant indicated by * (nonpair 't' test at 0.05 level).

Plant part and location	State of flowers	Soil surface	Opened flower	Unopened flower	Air at open flower
Plant No. 1 1030 hr June 25, 1978. SE-facing side with sand deposition	mostly open	25.8±0.3*	30.1±0.3*	28.0±0.6	28.3±1.8*
NW-facing side with sand deposition	most closed	22.6±0.3	27.2±0.5	26.9±0.9	25.2±0.3
Plant No. 2 1100 hr June 25, 1978 SE-facing side with sand deposition	mostly open	30.1±0.3*	31.0±0.3	30.5±0.6	32.1±0.5*
NW-facing side with sand deflation	all closed	26.7±0.6	--	27.5±0.4	27±0.6

Vegetative shoot growth originated from apical and subapical buds. Only very rarely did vegetative growth originate from shoots older than 1 yr. Each vegetative shoot grew to at least 1 cm before any secondary branching or bud formation was evident. For longer shoots, the location of secondary branching or bud formation was approximately 1 cm from the apex (Fig. 11). Bud formation occurred as early as late June and was most evident in late July and early August Shoot expansion of these secondary buds in the same year as their formation, only occurred in the most vigorous Hudsonia plants. Most buds grew to a length of 0.5 to 1 mm by mid-August The majority of vegetative growth was finished by mid to late July (Fig. 11). Fall colour developed as early as mid-July and was prominent in late July and throughout August Change to fall colouration was initiated at soil surface and proceeded up to the apex with time. At the Blowout, all phenologic events occurred earlier in the 1977 season than in 1978.

Production and carbon allocation strategy

Hudsonia biomass and production were intensively sampled at the Blowout site in 1978 (Table 15). Significant differences in growth patterns were found at the Blowout. Greatest total aboveground biomass per m^2 occurred in the Hudsonia-lichen (530 $g.m^{-2}$) and lichen removed (494 $g.m^{-2}$) communities. Biomass was significantly less in Hudsonia-sand communities. For example, the strongly depositional sand community had the largest biomass (201 $g.m^{-2}$) and the sand community without standing dead the smallest (34 $g.m^{-2}$).

Table 15. *Hudsonia* biomass, net annual production and carbon allocation in different site types within the Blowout, 1978. Mean ±95% confidence interval separation within columns by Duncan's Multiple Range test at the 5% level, n = 6.

Site	Number of twigs across sand-air interface (#.m^{-2})	Number of vegetative shoots (#.m^{-2})	Number of reproductive shoots (#.m^{-2})	Net annual production (g.m^{-2})	Previous years' growth (g.m^{-2})	Net annual production per amount of previous years' growth
Hudsonia lichen community	1496 ± 1317 c	76974 ± 26540 a	31286 ± 22999 a	199.2 + 148.3 a	331.0 + 251.4 a	0.69 ± 0.30 b
Hudsonia lichen community lichen removed	1327 ± 1432 c	46157 ± 19595 b	19449 ± 10542 a	123.7 ± 81.1 a	370.6 ± 303.4 a	0.38 ± 0.10 b
Hudsonia sand community with standing dead	2959 ± 2869 bc	18502 ± 15761 c	3939 ± 4563 b	37.1 ± 29.8 b	50.0 ± 51.1 b	1.03 ± 0.62 b
Hudsonia sand community without standing dead	4047 ± 1600 b	7449 ± 3944 c	851 ± 761 b	14.5 ± 7.8 b	19.5 ± 10.3 b	0.88 ± 0.50 b
Hudsonia sand community at base of depositional slope	4388 ± 906 b	6837 ± 2764 c	647 ± 285 b	28.6 ± 30.0 b	24.9 ± 29.6 b	2.04 ± 1.30 a
Hudsonia sand community strongly depositional	9761 ± 991 a	49729 ± 20334 b	5204 ± 1400 b	129.5 ± 16.2 a	71.4 ± 21.2 b	1.91 ± 0.51 a

The Hudsonia-lichen communities and the strongly depositional sand community had significantly greater amounts of net annual production than other communities. A similar trend was found for amount of previous years' growth except that the strongly depositional sand community had significantly less than the lichen community and was similar to other sand communities. The two Hudsonia communities associated with the depositional slope had the greatest ratio of net annual production to amount of previous years' growth (1.9 and 2.0, respectively) (Table 15). The Hudsonia-lichen and other sand communities had similar ratios, ranging from 0.38 to 1.03.

The Hudsonia-lichen communities had the greatest number of reproductive shoots, 31,286 and 19,449 per m^2 for the lichen and lichen removal communities, respectively (Table 15). The sand communities had significantly fewer reproductive shoots. The Hudsonia-lichen community had the greatest number of vegetative shoots per m^2 (76,974) followed by the lichen removal and strongly depositional sand communities (46,157 and 49,729 respectively), and then the other sand communities (6,837 to 18,502).

The density of twigs crossing the sand-air interface was less in the lichen and the sand with standing dead communities than in the other sand communities (Table 15). Density was greatest in the Hudsonia-strongly depositional sand community (9,761 per m^2).

At the Dune, aboveground net annual production was recorded for the mid-dune transect. Total aboveground plant biomass, net annual production and the ratio of net annual production to amount of previous years' growth varied along the 'successional' transect from open dune into the Pinus-lichen woodland (Fig. 12). For locations with greater than 2.5 $g.m^{-2}$ net annual production, the amount of net annual production was statistically similar along the transect ranging from 5.8 to 10.9 $g.m^{-2}$ except at meters 55 and 60 which had 16.9 and 22.2 $g.m^{-2}$. These two locations were at the transition from Hudsonia-sand community with standing dead to a Hudsonia-sand community with attached lichens. The pattern of total aboveground plant biomass followed that of net annual production. Total aboveground biomass was significantly greater at meters 55 and 60 than at other locations along the transect (analysis on locations with greater than 2.5 $g.m^{-2}$). The ratio of net annual production to previous years' growth, at 15 and 20 m from the open dune, was significantly greater than at other locations along the transect (ranging from 0.2 to 1.5). Only at meters 35, 40 and 60 were significant amounts of reproductive shoots found. They had 137, 374 and 680 reproductive shoots per m^2, respectively. Meters 55 and 60 had significantly greater numbers of vegetative shoots per m^2 (9,694 and 12,108, respectively). Numbers of vegetative shoots per m^2 ranged from 34 to 6,667 at other locations along the transect.

Root biomass was not measured in these studies. However, roots were found to be concentrated at a depth of 7 to 28 cm and extended down to at least 56 cm under plants in a Hudsonia-sand community at the Blowout (Fig. 13).

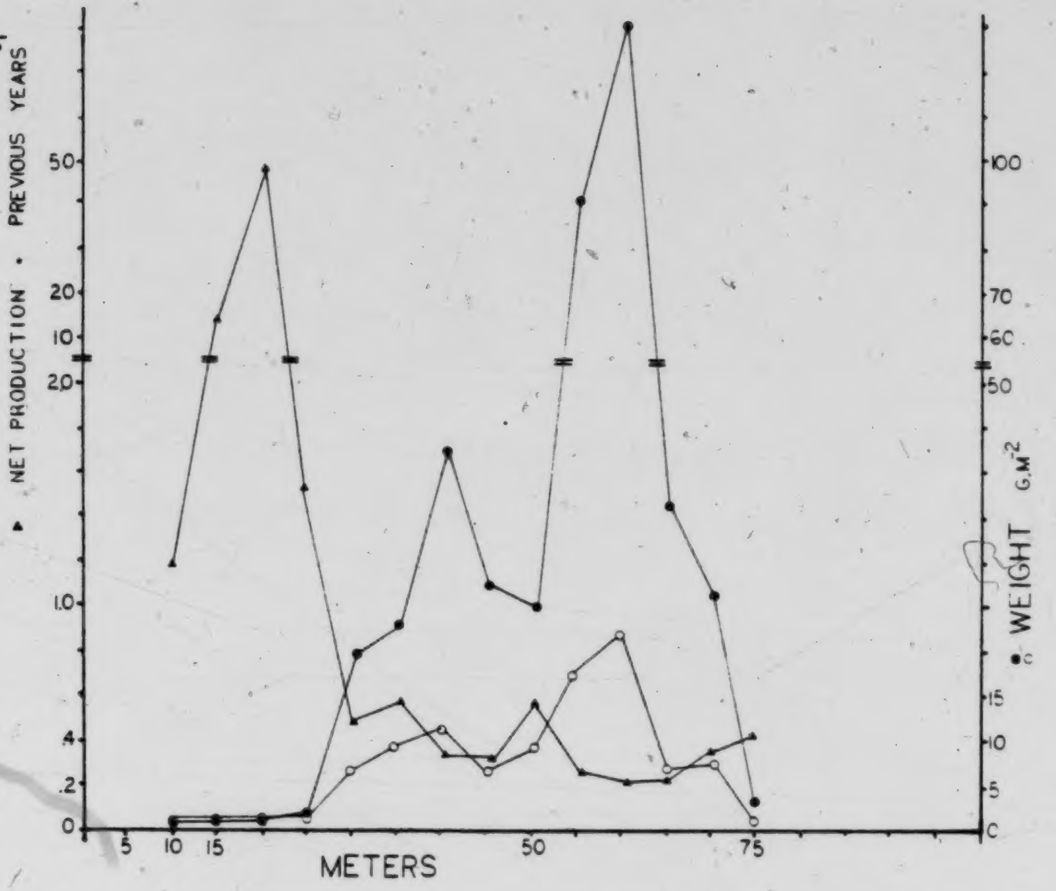


Figure 12 Net annual production and biomass of Hudsonia in 1978 at the Dune site. Data are for the mid-dune field transect from open sand into Pinus-lichen woodland along western edge of Maybelle River Dune System. Net annual production (○), biomass (●), and ratio of net annual production to previous years' growth (▲) were sampled August 23, 1978, n=6.

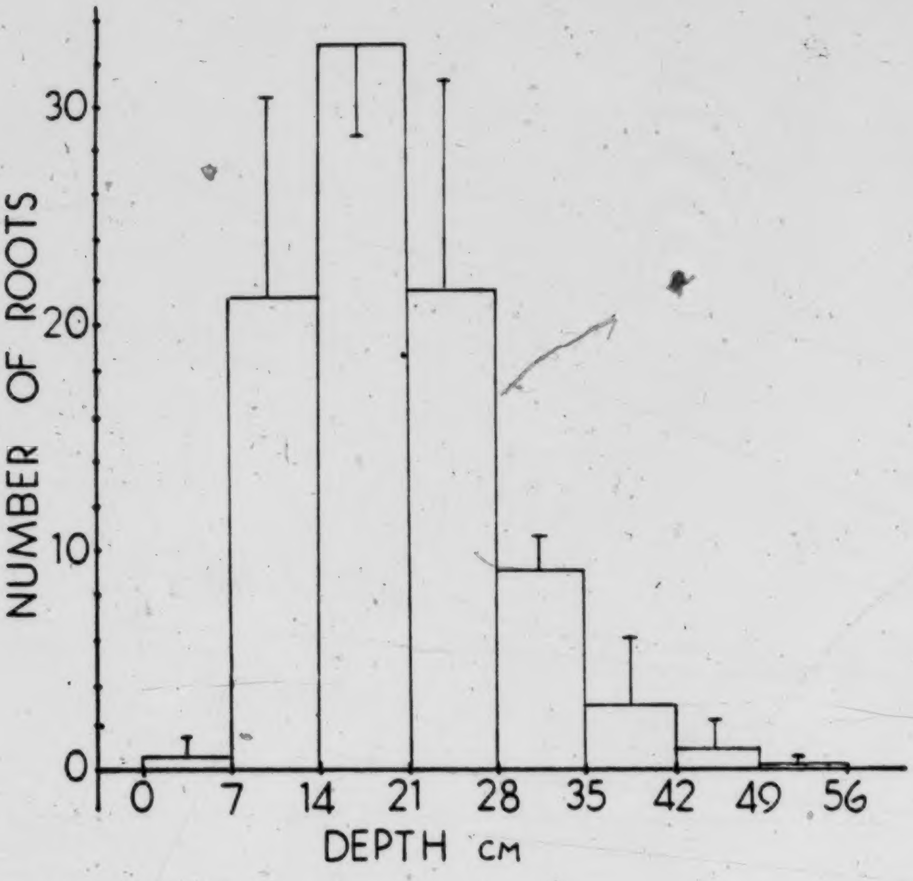


Figure 13 Location of roots under a Hudsonia-sand community. Each value is an average of 7 plants +95% confidence level in which a 7 cm by 21 cm rectangle was analyzed at each depth for number of roots visible in a vertical profile centered through the plant.

Significant differences between years and sites were found for carbon allocation and net annual production in individual plants (Table 16). The same seven plants per site were measured in each of the three years. Plants in 1978 had a greater number of vegetative shoots (34.8), greater allocation to reproduction (49.2%) and greater amount of reproductive growth per amount of previous years' growth (1.1) as compared to 1977 and 1979. Plants in 1979 had greater total and mean lengths of vegetative shoot growth (16.7 cm and 7.7 x 10^{-1} cm, respectively), greater amounts of last year and previous years' growth (30.2 x 10^{-3}g and 38.4 x 10^{-3}g. plant^{-1}. respectively), and smallest reproductive shoot growth per amount of previous years' growth (0.2) as compared to 1977 and 1978. Plants in 1977 had smaller allocation to reproductive growth (5.2%), smaller amounts of previous years' and last year growth (8.0 x 10^{-3}g and 4.4 x 10^{-3}g, respectively), greater vegetative growth and net annual production per amount of previous years' growth (15.4 and 15.8, respectively) as compared to 1978 and 1979. In 1978, carbon allocation to reproductive growth was 50%, by early July. (Fig. 14).

Individual plants in the Hudsonia-strongly depositional sand community had significantly greater total length of vegetative shoot growth per plant (29.0 cm), number of vegetative shoots per plant (37.3), mean length of vegetative shoots (8.1 cm), allocation to vegetative growth (91.9%), net annual production per plant (76.3 x 10^{-3}g), and greater vegetative shoot growth and net annual production per amount of previous years' growth (16.5 and 16.8,

Table 16. Influence of year and site-type on Hudsonia growth and carbon allocation at the Blowout. The same 7 plants were measured over a 3 year period in 5 sites; Hudsonia-lichen community (1), Hudsonia-cyclic sand deflation and deposition community (2), Hudsonia-sand deflation with standing dead community (3), Hudsonia-sand deposition without standing dead community (4) and Hudsonia-strongly depositional sand community (5). Mean separation within YEAR and SITE rows by Duncan's Multiple Range Test at the 0.05 level.

	Year			Site				
Plant variable	1977	1978	1979	1	2	3	4	5
Net annual production per plant ($g.10^{-3}$)	18.7 b	46.6 a	46.5 a	25.1 b	24.8 b	31.0 b	26.0 b	76.3 a
Allocation to vegetative growth (%)	94.8 a	50.8 c	85.0 b	69.9 b	75.4 b	73.7 b	73.6 b	91.9 a
Allocation to reproductive growth (%)	5.2 c	49.2 a	15.0 b	30.1 a	24.6 a	26.3 a	26.4 a	8.1 b
Mean length of vegetative shoot growth per plant ($cm.10^{-1}$)	4.5 b	3.2 b	7.7 a	4.4 b	5.0 b	3.4 b	4.9 b	8.1 a
Total length of vegetative shoot growth per plant (cm)	8.2 b	11.9 b	16.7 a	6.3 b	8.6 b	9.6 b	8.1 b	29.0 a
Total number of vegetative shoots per plant (#)	18.4 b	34.8 a	23.7 b	21.7 b	19.4 b	29.6 as	20.0 b	37.3 a
Weight of previous years' growth per plant ($g.10^{-3}$)	8.0 c	20.2 b	38.4 a	23.7 b	14.7 c	28.7 ab	9.6 c	34.2 a
Weight of last year growth per plant ($g.10^{-3}$)	4.4 c	14.1 b	30.2 a	11.8 bc	12.6 bc	15.7 b	8.2 c	33.0 a
Vegetative shoot growth per amount of previous years' growth ($g.g^{-1}$)	15.4 a	1.8 b	1.3 b	1.1 b	6.0 b	0.9 b	6.2 b	16.5 a
Reproductive shoot growth per amount of previous years' growth ($g.g^{-1}$)	0.5 b	1.1 a	0.2 c	0.4 b	1.0 a	0.3 b	0.8 a	0.3 b
Net annual production per amount of previous years' growth ($g.g^{-1}$)	15.8 a	2.9 b	1.5 b	1.5 b	7.0 b	1.2 b	7.0 b	16.8 a

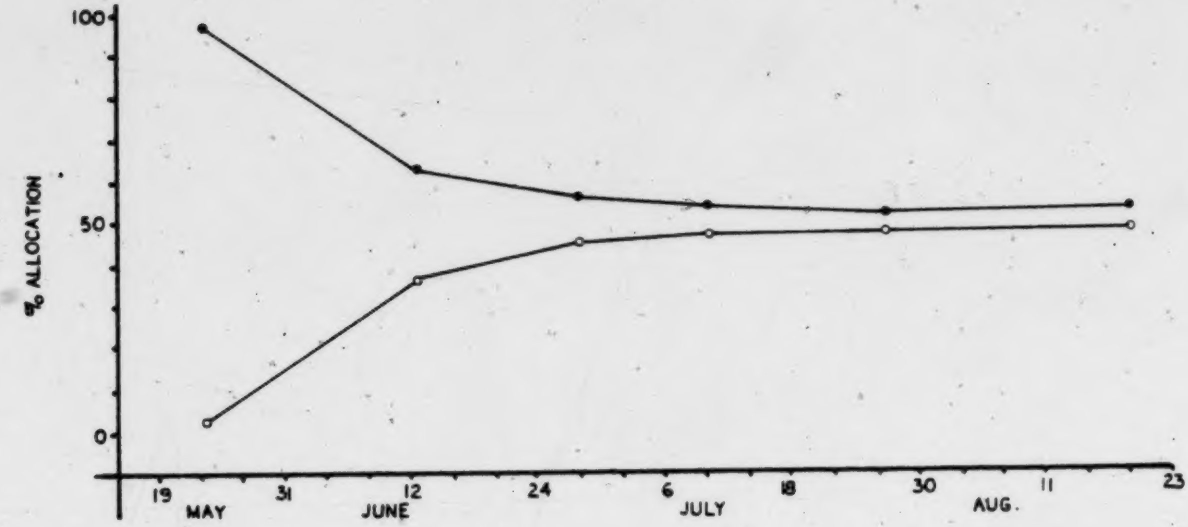


Figure 14 Hudsonia carbon allocation throughout the 1978 field season at the Blowout. Vegetative growth (●) initially included preformed buds which become reproductive shoots and were included in reproductive allocation (○) through the season even after fruit fall. Each data point represents the mean of 35 plants.

respectively) as compared to other sites (Table 16). Other sites tended to be similar to each other, however, the Hudsonia-sand communities without standing dead or with cyclic sand deflation and deposition had significantly less previous and last year growth per plant.

Regression of amount of burial per plant, height of first vegetative growth aboveground, amount of last year growth per plant, and amount of standing dead per plant were analyzed against dependent plant variables (Table 17). These independent plant variables were introduced in a step-wise manner such that the next variable included reduced the residual variance by the greatest amount. The equations in Table 17 include only independent variables which significantly reduced the residual variance. The amount of burial was positively correlated with net annual production per plant, percent allocation to vegetative growth, mean and total length of vegetative growth, and with the amount of vegetative shoot growth and net annual production per amount of previous years' growth (Table 17). The amount of burial was negatively correlated with the amount of reproductive growth. The amount of last year growth was positively correlated with the total number of vegetative shoots, total length but not mean length of vegetative shoots, and net annual production per plant (Table 17). The amount of last year growth was negatively correlated with vegetative shoot growth per amount of previous years' growth. The amount of last year growth had no significant correlation to the amount of reproductive shoot growth per amount of previous years'

Table 17. Multiple regression of site variables versus plant variables, for all sites and years at the Blowout site. Only site variables with significant reduction on residual variance are included. Site variables tested were amount of last year growth remaining in current year (LAST YEAR, g. plant $^{-1}$), amount of sand deposition per plant since the start of the current season (BURIAL, cm.), amount of standing dead aboveground (SD, g. plant^{-1}), height of first vegetative growth above the ground (HT, cm.), degree days since start of season (DEGDAY, 5°C threshold from April 23 to August 26, 1977, April 24 to August 18, 1978, and April 23 to August 03, 1979 at Richardson Fire Tower), and total precipitation (TPPT, cm.). Total n = 105, with the same 35 plants measured over the 3 years, 1977, 1978 and 1979. Analysis b includes degree day and total precipitation, whereas a does not. Only one equation is given when analysis a equalled analysis b. Mean values for independant variables were BURIAL = 0.604 cm. plant $^{-1}$, LAST YEAR = 16.0X10^{-3} g. plant^{-1}, SD = 22.0 x 10^{-3} g. plant $^{-1}$, HT = 2.74 cm plant $^{-1}$, DECD = 1024° and TPPT = 181.3 mm.

Plant variable	Significant site factor regression	Correlation coefficient
Net annual production per plant ($g.10^{-2}$)	1.70 + 70.35 LAST YEAR + 1.38 BURIAL	0.720
Allocation to vegetative growth (%)	a. 76.10 + 11.34 BURIAL - 284.08 SD b. -605.6 + 10.54 BURIAL + 0.81 DEGDAY -0.86 TPPT	0.422 0.627
Allocation to reproductive growth (%)	a. 23.90 - 11.34 BURIAL + 284.08 SD b. 706.0 - 10.53 BURIAL - 0.81 DEGDAY + 0.86 TPPT	0.422 0.627
Mean length of vegetative shoot growth per plant ($cm.10^{-1}$)	3.98 + 1.87 BURIAL	0.535
Total length of vegetative shoot growth per plant (cm)	4.77 + 7.43 BURIAL + 185.89 LAST YEAR	0.789
Total number of vegetative shoots per plant (#)	19.55 + 375.70 LAST YEAR	0.432
Vegetative shoot growth per amount of previous years' growth ($g.g^{-1}$)	a. 9.41 - 0.55 HT - 356.70 LAST YEAR + 6.50 BURIAL b. -88.19 + 0.09 DEGDAY + 7.82 BURIAL - 244.16 LAST YEAR	0.527 0.611
Reproductive shoot growth per amount of previous years' growth ($g.g^{-1}$)	0.96 - 0.31 BURIAL - 0.07 HT	0.349 0.209
Net annual production per amount of previous years' growth ($g.g.^{-1}$)	a. 9.74 - 312.50 SD + 6.35 BURIAL b. -86.47 + 0.09 DEGDAY + 7.67 BURIAL - 247.43 LAST YEAR	0.507 0.606

growth, mean length of vegetative shoot growth per plant, and allocation to reproductive or vegetative growth. The amount of standing dead was positively correlated with allocation to reproductive growth, and, was negatively correlated with allocation to vegetative growth and net annual production per amount of previous years' growth. Height of first growth was negatively correlated with the amount of vegetative and reproductive shoot growth per amount of previous years' growth.

The introduction of degree-days and total precipitation into the regression analysis only resulted in minor changes to the allocation equations, and to the vegetative shoot growth and net annual production per amount of previous years' growth equations. Allocation to vegetative shoot growth was positively correlated with degree-days and negatively correlated to total precipitation. Both vegetative shoot growth and net annual production per amount of previous years' growth were positively correlated to degree-days.

Sand burial and lichen removal experiments

Burial treatments were maintained at a mean (for all sites) level of 0.02 and 1.13 cm in 1977 and 0.003, 2.01 and 4.33 cm in 1978 (Table 18). These values represent mean end of season (August 26, 1977 and August 19, 1978) deposition based on readings taken at the start of the experiments on July 24, 1977 and May 26, 1978. Some cyclic sand deflation and deposition occurred between servicing the experiments on a weekly basis.

Table 18. Degree of sand deposition in the sand burial experiments at the Blowout. Mean of 3 reps for amount of deposition for the period July 24 to Aug 26 in 1977 and May 26 to Aug 19 in 1978. The buried glass slide technique was used in Hudsonia-lichen community (1), Hudsonia-sand community with standing dead (2), Hudsonia-sand community without standing dead (3) and the Hudsonia-sand community at the base of a strongly depositional slope (4).

Site	Control (cm)	2X (cm)	4X (cm)
(a) 1977			
2	0.4	1.7	--
3	-0.2	0.8	--
4	-0.2	0.9	--
$\bar{X}$ ± 95% Confidence limits	0.02±0.53	1.13±0.73	
(b) 1978			
1	0.31	2.05	5.01
2	-0.45	2.50	4.80
3	0.10	1.80	3.00
4	0.05	1.70	4.50
$\bar{X}$ ± 95% Confidence limits	0.003±0.51	2.01±0.57	4.33±1.45

In 1977, no significant effects of sand deposition were detected (Table 19). Significant differences between sites were found. Hudsonia-sand communities without standing dead had greater net annual production, and, vegetative and reproductive shoot growth per amount of previous years' growth than did communities with standing dead.

In 1978, significant effects of burial and sites on Hudsonia performance were found (Table 20). Sand deposition caused significant increases in mean length of vegetative shoot growth per plant, and in the amount of net annual production, and vegetative shoot growth per amount of previous years' growth (Table 20 and Fig. 15). Sand deposition had no significant effect on number of flowers per plant, reproductive shoot growth per amount of previous years' growth, or allocation to reproductive or vegetative shoot growth. Several significant linear regressions were derived showing the relationship between sand deposition and Hudsonia performance (Table 21). No significant relationship was described for the effect of burial on allocation to vegetative shoot growth. However, a trend of increasing allocation to vegetative shoot growth with increasing sand deposition was noted (Table 20). A linear regression of this data (Fig. 16) indicated that percent vegetative shoot growth equals 61.0 plus 4.2 multiplied by the amount of sand deposition (cm). However, the data points indicated a more asymptotic response curve.

Significant site effects were found for number of flowers per plant, net annual production and reproductive growth per amount of previous years' growth, and in the allocation to reproductive or

Table 19. Effect of sand burial on Hudsonia performance, 1977 burial experiments. Split-plot ANOVA, mean separation within rows by Duncan's Multiple Range Test, 0.05 level. Site 1 was a Hudsonia-sand community with standing dead; 2 was a Hudsonia-sand community without standing dead; and 3 was a Hudsonia sand community at the base of a strongly depositional slope. Burial 1 was 0.24±0.53 cm, and 2 was 1.13±0.73 cm sand deposition for the time period July 24 to Aug 26. The amount of previous years' growth refers to that amount aboveground on July 24 before the experiment was started.

Plant variable	(a) Site			(b) Burial	
	1	2	3	1	2
Mean length of vegetative shoot growth per plant (cm)	0.38 a	1.17 b	1.95 c	0.79 a	1.54 a
Net annual production per amount of previous years' growth ($g.g^{-1}$)	1.1 b	7.2 a	23.7 a	8.7 a	12.6 a
Vegetative shoot growth per amount of previous years' growth ($g.g^{-1}$)	1.1 b	7.0 a	23.5 a	8.6 a	12.5 a
Reproductive shoot growth per amount of previous years' growth ($g.g^{-1}$)	0.021 b	0.13 a	0.13 a	0.09 a	0.09 a

Table 20. Effect of sand burial on *Hudsonia* performance, 1978 burial experiments. Split-plot ANOVA, mean separation within rows by Duncan's Multiple Range test, 0.05 level. Site 1 was a *Hudsonia*-lichen community; 2 was a *Hudsonia*-sand community with standing dead; 3 was a *Hudsonia*-sand community without standing dead; and 4 was a *Hudsonia* sand community at the base of a strongly depositional slope. Burial 1 was 0.003$\pm$0.51 cm, 2 was 2.01$\pm$0.57 cm, and 3 was 4.33$\pm$1.45 cm sand deposition for the time period May 26 to Aug 19 (Table 10). The amount of previous years' growth refers to that amount aboveground on May 26.

	(a) Site				(b) Burial		
Plant variable	1	2	3	4	1	2	3
Mean length of vegetative shoot growth per plant (cm)	0.78 a	0.95 a	0.62 a	0.90a	0.46 b	0.74 ab	1.23 a
Number of flowers per plant	14.7 a	5.7 bc	3.3 bc	10.4 ac	8.0 a	8.3 a	9.0 a
Net annual production per amount of previous years growth ($g.g^{-1}$)	7.4 a	5.2 a	3.5 b	3.7 b	2.3 b	5.3 ab	7.3 a
Vegetative shoot growth per amount of previous years' growth ($g.g.^{-1}$)	5.2 a	4.7 a	2.6 a	3.1 a	1.4 a	4.0 a	6.3 b
Reproductive shoot growth per amount of previous years' growth ($g.g.^{-1}$)	2.2 a	0.5 b	0.9 b	0.6 b	0.9 a	1.3 a	1.0 a
Percent allocation to vegetative shoot growth (%)	54 b	84 a	57 b	82 a	58 a	71 a	77 a
Percent allocation to Reproductive shoot growth (%)	46 a	16 b	43 a	18 b	42 a	29 a	23 a

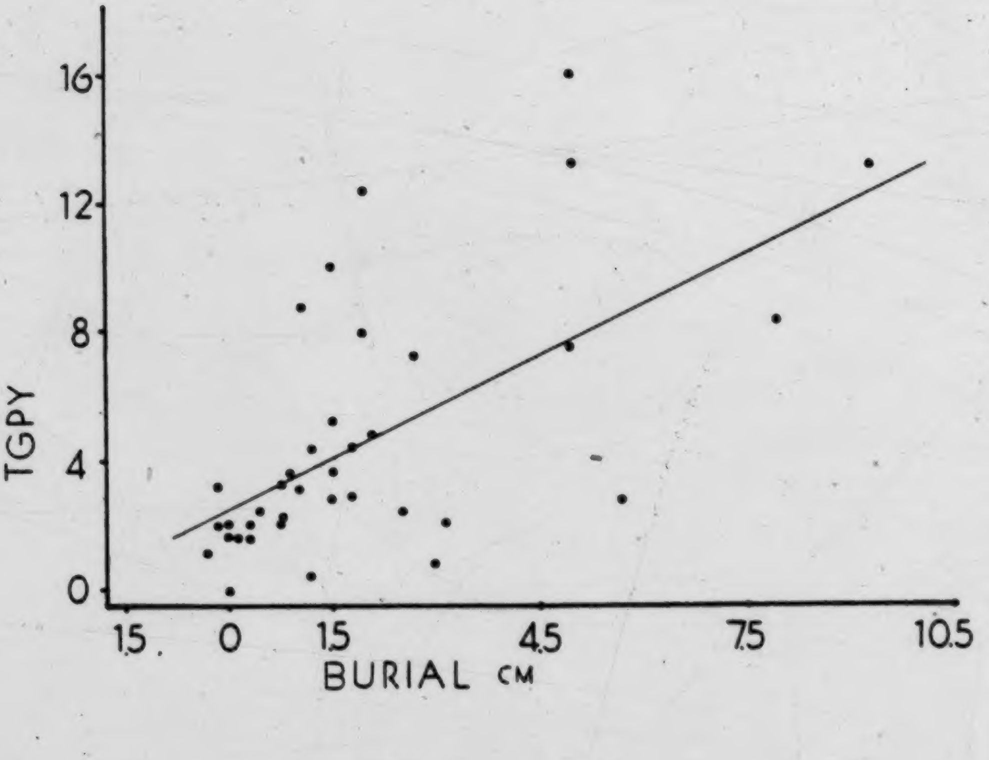


Figure 15 The influence of sand burial on net annual production 1978 burial experiment. Net annual production per amount of previous years' growth (TGPY), and the amount of sand burial for a particular plant at end of season, August 19, 1978 are indicated. Data are for all sites (4), all treatments (3) and all reps (3). Regression of TGPY versus amount of sand burial, is $Y = 2.59 + 1.15X$, $r_{xy} = 0.635$.

Table 21. Linear regressions for significant effects of sand burial on Hudsonia, 1978. Burial level measured on a per plant basis, correlation coefficient is rxy.

Site	Y		A (Y intercept)		B (amount of burial, cm)	N	r_{xy}
(a)							
All	Net annual production per amount of previous years' growth ($g.g^{-1}$)	=	2.59	+	1.15	36	0.64
	Vegetative shoot growth per amount of previous years' growth ($g.g^{-1}$)	=	1.60	+	1.18	36	0.66
	Mean length of vegetative growth per plant (cm)	=	0.423	+	0.07	36	0.45
(b)							
Hudsonia-lichen and sand community with standing dead	Net annual production per amount of previous years' growth ($g.g^{-1}$)	=	3.129	+	1.14	18	0.66
(c)							
Hudsonia-sand community, at base of deposition slope, and without standing dead	Net annual production per amount of previous years' growth ($g.g^{-1}$)	=	3.35	+	0.174	18	0.88

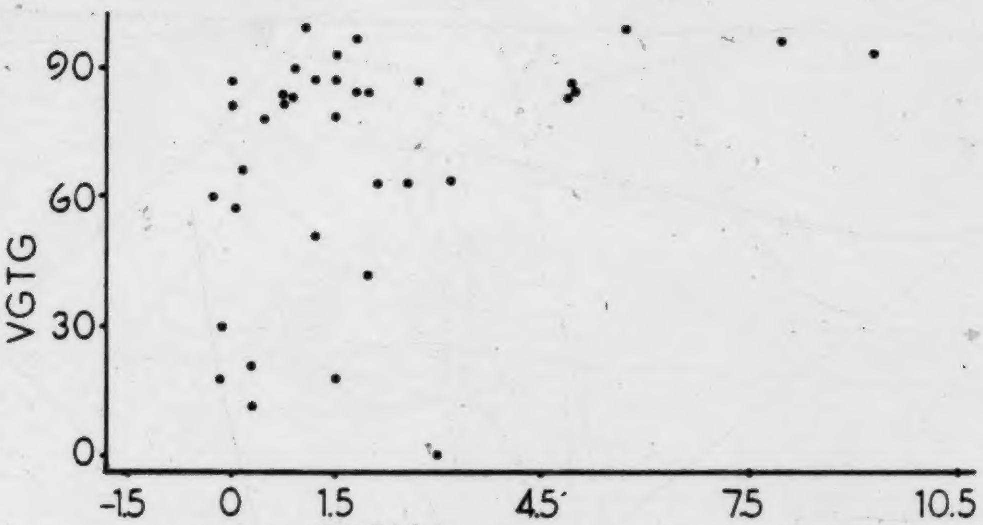


Figure 16 The influence of sand burial on percent allocation to vegetative shoot growth (VGTG), 1978 burial experiments. Amount of sand burial for a particular plant at end of season (BURIAL) was recorded on August 19, 1978. Data are for all treatments (3), all reps (3) and all sites (4), r_{xy} = 0.347.

vegetative shoot growth (Table 20). The number of flowers per plant was greatest in the *Hudsonia*-lichen community and the *Hudsonia*-sand community at the base of a strongly depositional slope. Net annual production per amount of previous years' growth was greatest in communities with standing dead. Reproductive shoot growth per amount of previous years' growth was greatest in the *Hudsonia*-lichen community. Allocation to vegetative growth was greatest in *Hudsonia*-sand communities with standing dead, and those at the base of a strongly depositional slope. Allocation to reproductive growth was greatest for the *Hudsonia*-lichen community and the *Hudsonia*-sand community without standing dead.

Data from statistically similar sites in which sand burial had significant effects were grouped (Table 21). Net annual production per amount of previous years' growth in sites without previous sand deposition (*Hudsonia*-lichen and sand community with standing dead) equals 3.13 plus 1.14 multiplied by the amount of burial (cm). When data for these sites were split, greater correlation coefficients were obtained (Fig. 17). The correlation coefficient was not significant for sites which had previously experienced sand deposition (*Hudsonia*-sand communities without standing dead, and at the base of a strongly depositional slope).

The removal of all lichen from a 5 by 5 m area in a *Hudsonia*-lichen community caused a significant increase in mean length of vegetative shoot growth per plant, vegetative shoot growth per amount of previous years' growth, and allocation to vegetative growth

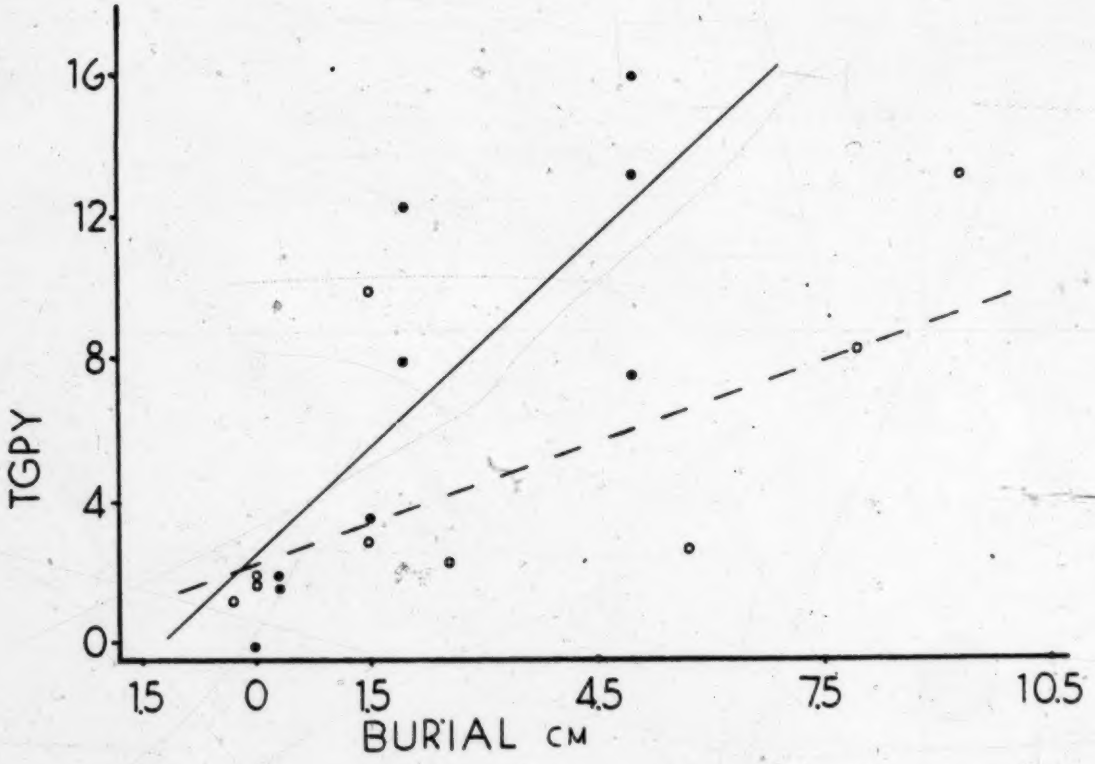


Figure 17 The influence of sand burial on vegetative shoot growth per amount of previous years' growth in selected sites at the Blowout in the 1978 burial experiments. Vegetative shoot growth per amount of previous years' growth (TGPY) and amount of sand burial for a particular plant at end of season (BURIAL) are indicated for all treatments (3) and all reps (3). Sites are Hudsonia-lichen community (●) and Hudsonia-sand community with standing dead (○). Correlation coefficient for Hudsonia-lichen community was 0.831 and for Hudsonia-sand community with standing dead was 0.721.

(Table 22). Lichen removal caused a significant reduction in percent allocation to reproductive growth in relation to controls. No significant effects on number of flowers per plant, and net annual production or reproductive shoot growth per amount of previous years' growth were detected.

Seed germination and seedling ecology

Seeds of Hudsonia were found at all study sites, either on the plant, dehisced from the capsule or still in the abscissed fruit. Approximately 70% of the abscissed fruit contained seeds. Approximately 32% contained one apparently viable seed, 28% contained two apparently viable seeds, and 10% contained only degenerated seeds. Splitting the capsule open resulted in seed fall, however, naked seeds were only slightly wind dispersed as they tended to become wedged between sand grains. Fruits were wind dispersed along the sand surface up to distances equal to at least the width of the Maybelle River Dune System . Fallen fruit tended to collect around debris, in foot-prints, in hollows and bowls, and at the base of depositional slopes (Plate 8). Forty such collections were sampled at the Dune site and found to have a mean diameter of 7.3 ± 1.1 cm. The largest collection of fallen fruit was 38 cm in diameter and contained an estimated 29,250 fruits.

Germinated seeds were generally not found in Hudsonia-sand communities with excessive sand deflation and deposition, in Hudsonia-lichen communities, or along the eastern edge of the Maybelle

Table 22. Influence of lichen removal on Hudsonia performance, 1978 Blowout sites. Lichens removed Aug. 1, 1977 and data recorded Aug 19, 1978. Mean of 7 values, ±95% confidence level, and mean separation within rows by unpaired 't' analysis at 0.05 level. The amount of previous years' growth refers to the amount above ground on May 26, 1978.

Plant variable	Experimental condition	
	Lichen	Lichen removed
Mean length of vegetative shoot growth per plant (cm)	0.14±0.02 a	0.34±0.14 b
Number of flowers per plant	10.1 ±7.7 a	6.4 ±4.4 a
Net annual production per amount of previous years' growth ($g.g^{-1}$)	0.91±0.53 a	0.81±0.52 a
Vegetative shoot growth per amount of previous years' growth ($g.g^{-1}$)	0.12±0.09 a	0.44±0.28 b
Reproductive shoot growth per amount of previous years' growth ($g.g^{-1}$)	0.79±0.42 a	0.37±0.32 a
Percent allocation to vegetative shoot growth (%)	14.0 ±6.8 a	60.0±20.9 b
Percent allocation to reproductive shoot growth (%)	86.0± 6.9 a	40.0±23.2 b

Plate 8 Collections of Hudsonia seedlings and fruits. This hollow contained several layers of buried fruits. The seedlings (1 and 2 yr) originate from buried fruit 1-4 cm below the surface.

COLOURED PICTURES
Images en couleur

River Dune System. Seedling numbers were greatest in Hudsonia-sand communities at both study sites (Tables 23 and 24). Seedlings were not found in the Hudsonia-lichen removal plots even though a local seed source was available (Table 23). Groups of seedlings were frequently observed, and were always associated with a collection of buried fruit at depths of 1-4 cm (Plate 8).

Seed germination and seedling emergence took place mainly before May 25th in 1978, but also occurred during July and August (Table 23). In no case was germination of current year seed observed in the field, however, these seeds germinated in the lab without any cold pretreatment. Laboratory experiments indicated that high water potentials were required for germination after imbibition in distilled water (Table 25), and that, imbibition could not be achieved unless the thick hard seed coat was sanded with medium grained sand paper.

Seedling mortality in the first year was high (Table 23), with an average of 80% loss at the mid-dune site (Table 24). Seedling mortality occurred during summer months and between field seasons (Table 23).

Seedling age had a significant effect on aboveground biomass (Table 26). Plants older than 2 yr, had greater aboveground biomass (466.5 mg per plant) than either 1 to 2 yr olds (95.4 mg per plant) or plants less than 1 yr old (4.7 mg per plant). Root to shoot ratio decreased as plants aged (0.72 ± 0.19 for the 1 yr seedlings to 0.26 ± 0.08 for plants greater than 2 yr in a Hudsonia-sand community at the base of a strongly depositional slope).

Table 23. Influence of site type and sample date on *Hudsonia* seed germination and seedling fate, 1977-1978 Blowout site. Mean ±95% confidence interval separation within columns at the 0.05 level, n = 10.

(a) Influence of site type on 1978 seedlings (#.m^{-2})

Site	Number of 1978 seedlings August 15, 1978	Number germinated after July 08, 1978
Hudsonia- lichen community	0.1±0.7 b	0.0 b
Hudsonia- lichen removal plot	0.2±0.9 b	0.0 b
Hudsonia- sand community with cyclic sand deposition and deflation	6.2±3.2 a	1.5±0.5 a
Hudsonia- sand community at base of strongly depositional slope	4.2±2.7 a	2.0±1.1 a

(b) Influence of time on seedlings (#.m^{-2}) in the *Hudsonia* sand community with cyclic sand deposition and deflation.

Seedling germination date	Sample date			
	Aug. 11, 1977	July 8, 1978	Aug. 15, 1978	Net change
1976	0.6±0.9	0.5±1.1	0.5±1.1	-0.1±0.2
1977	2.2±2.3	0.9±1.4	0.9±1.4	-1.3±1.6
1978	-	11.0±4.3	6.2±3.2	-4.8±3.8
After July 8, 1978	-	-	1.5±0.5	-

Table 24. Number of Hudsonia seedlings along a transect from open dune to Pinus-lichen woodland, Dune site.

Distance from open dune (m)	Total seedlings ($\#.m^{-2}$) 1976-77-78	Number 1978 seedlings in 1978 ($\#.m^{-2}$)	Number 1978 seedlings in 1979 ($\#.m^{-2}$)
0	3	0	0
5	9	6	0
10	8	3	1
15	14	10	2
20	18	10	3
25	0	0	0
30	0	0	0
35	1	0	0
40	0	0	0
45	1	0	0
50	0	0	0
55	0	0	0
60-125	0	0	0

Table 25. Influence of solution water potential (MPa) on Hudsonia seed germination. Treatment in PEG 6000, after seed imbibition, n = 3 for 30 seeds each. Mean +95% confidence interval separation within columns at 0.05 level.

Water potential (MPa)	Seed germination (%)
-0.0	57 ± 19.5 a
-0.1	63 ± 12.3 a
-0.3	7 ± 16.2 b
-0.6	0 b
-1.5	0 b

Table 26. Root: shoot ratio and biomass of *Hudsonia* seedlings in 1978. Mean separation within a site by unpaired 't' test at 0.05 level. Mean values ±95% confidence level for *Hudsonia*-sand community at the base of a strongly depositional slope (1), dune flats western edge of Maybelle River Dune System (2) and *Hudsonia*-sand community with standing dead and wind caused sand deflation (3).

Site	Seedling age (yr)	Aboveground biomass (mg. plant^{-1})	Root: shoot ratio (g.g^{-1})	n
1	less than 1	4.67 ± 0.70 a	0.72 ± 0.19 a	12
	between 1 and 2	95.37 + 35.57 b	0.34 ± 0.08 b	12
	greater than 2	466.50 ± 135.56 c	0.26 ± 0.08 b	12
2	less than 1	1.04 ± 0.22	1.00 ± 0.25	12
3	greater than 2	229.80 ± 146.36	0.20 ± 0.05	12

DISCUSSION

Several important phenologic observations and growth measurements were made which relate to the ability of Hudsonia to colonize these northern sand dune and blowout areas. Plant greening up occurred soon after snow-melt, however, bud expansion was delayed until mid to late May. Many preformed buds had greened up and were likely to carry out significant net assimilation prior to bud expansion. Net assimilation in last year tissue was unlikely as leaves remained tan to brown coloured. Initial bud expansion was limited to short reproductive shoots. These shoots presumably support the initial and subsequent carbohydrate demand of the reproductive structures and provide nutrients for recycling as they degenerate after fruit fall. The initial stage of reproductive bud expansion preceded initial stages of vegetative bud expansion, but was then synchronized to vegetative bud expansion. Flower opening occurred before other vascular plant species provided significant competition for bee visitations and pollinations. Also, a significant portion of the growing season remained for fruit development, including the copious endosperm (30-60 d). Flower opening was correlated with elevated temperatures (Table 14), thus ensuring that flowers did not open before pollinators were active. Morse (1979) also noted the sequential pattern of flower opening from the sand surface upwards. However, in his study, Hudsonia flowers only remained open for 1 d due to the wilting of petals. He also noted a concentrated period of Hudsonia flower opening in mid-June, as was found in this study. He concludes that temperature, rather than daylength, controls flowering (inland plants flower earlier than coastal plants at the same latitude) and that, insect cross-pollination in Hudsonia is not obligatory for seed set due to the possibility of autogamy and selfing. It may be that the limited number of alternate hosts at my study sites ensures bee visitations. It remains to be determined what role these visitations play in the breeding system of Hudsonia.

At the time of fruit fall, most capsules contained at least one apparently viable seed. Fruit fall occurred after seed development was completed and early enough that wind dispersal and sand burial could take place in the current year.

Approximately 90% of vegetative shoot growth was completed by mid to late July in 1978. After this period, vegetative shoot growth was mostly restricted to bud formation. Although fall coloration and limited leaf abscission took place throughout August, it is likely that significant nutrient relocation and photosynthate allocation to root systems took place under these suitable temperature, light and moisture growing regimes. This early cessation of shoot growth is adaptative in order to prevent exposure of tender tissues to potential early frosts. Longley and Janz (1978) indicated a NORM of 1 frost period in August and 9 in September Photoperiodically controlled stages of plant dormancy were likely to be involved in this early cessation of growth (Levitt, 1972). However, in the fall of 1976 an extended warm period in September allowed for greening up of preformed buds. The low percent allocation to reproduction in 1977 (Table 16) may in part be due to freezing damage of preformed reproductive buds which took place later in the fall of 1976.

The difference in timing of phenologic events in 1977 and 1978 relates to climatic conditions. In 1977, May was hot and wet (+4.5°C and +31.5 mm precipitation greater than NORMS) relative to the warm moist May (+1.1°C and +12.8 mm precipitation greater than NORMS) of 1978 (Table 3). This difference caused earlier vegetative growth and flowering in 1977, especially as early June in 1978 was cool.

The extent of vegetative sand colonization by individual Hudsonia plants was difficult to determine. The maximum single plant size observed was 59 cm diameter, however, twigs in mats not obviously connected to each other at the sand surface were connected at varying depths under the sand. Adventious rooting and underground separation of parts occurred. This clone-forming habit limited Hudsonia dispersal to distances of meters. The main method of plant dispersal was via wind dispersed, seed-containing fruit which were blown across the sands. The cause of significant numbers of degenerated seeds is unknown. Harper (1977) concludes that plants usually initiate many more seeds than can be eventually matured, and that adjustment in seed crop size is determined by prevailing circumstances. For example, the dry June and July in 1978 may have limited seed development. Fruit collections and concentrated numbers of seedlings were often associated with each other in depressions and around debris (Plate 8). Seedling numbers were reduced in Hudsonia-sand communities with excessive sand deposition and deflations, in Hudsonia-lichen communities, and along the eastern edge of the Maybelle River Dune System. Hudsonia-sand communities with moderate sand deposition and deflation contained larger numbers of seedlings (Table 23). Seeds which successfully germinated were always 2-4 cm under the sand surface, indicating the need for sand burial before imbibition and germination. Many seedlings remained attached to the fruit after emergence. Under excessive burial (>6 cm), radicle elongation would deplete the seed endosperm reserve before exposure to light for net assimilation. Soil water potentials of approximately 0.0 to -0.1 MPa were required for germination and successful seeding growth (Table 25). An accumulating number of wet and low temperature days such as in May would be required for these soil water potentials. The water absorbing and retention characteristics of the pubescent fruit in large buried collections may significantly improve the chance for successful imbibition, germination and growth. Another possible significance for large collections of buried seed containing fruit relates to the thick, hard seed coat of Hudsonia. Mechanical damage such as sand paper abrasion or freeze-thaw cycles were required to break up the seed coats for imbibition. Cold stratification of seed was not required for germination.

New seedlings were not found in Hudsonia-lichen communities due to limited sand burial and the lichen carpet. The lack of; a clone forming habit, successful seed dispersal and germination, and, vigorous growth in Hudsonia-lichen communities ensured that the Hudsonia-lichen 'successional' stage was short-lived (unless a disturbance occurred). Fire and blowouts would provide a more favourable environment for seed burial and subsequent germination. Therefore, the high percent allocation to reproductive growth in Hudsonia-lichen communities was most often a waste but ensured that Hudsonia would be competitive in terms of colonization when these sites were disturbed.

Seedling mortality in the first year was high at both the Blowout and Dune (Table 23 and 24). Losses take place during summer months and between summer seasons, probably due to dessication stress, and wind and sand abrasion.

Root:shoot ratios decreased with plant age, (Table 26), a trend consistent with that found in other shrubs (Whittaker, 1962). However, the ratio at 1 to 2 and greater number of years was low (0.34 to 0.26), compared with other dwarf ericaceous shrubs (0.60 to 0.70-Larcher, 1973). This ratio was more similar to that of evergreen conifers of the taiga and mountain forests, deciduous trees of the temporate zone and young conifers. Struik and Bray (1970) indicate that root:shoot ratios are higher in sites where water and nutrients are limiting. Possibly, desiccation and nutrient stress on Hudsonia plants older than 1 yr was not limiting. However, high seedling mortality in the first year may reflect a great susceptibility to desiccation stress, possibly due to the lack of water absorbing mycorrhizal associations which were present in greater than 2 yr old plants.

Annual net production for Hudsonia-sand and lichen communities at the Blowout and Dune sites ranged from 1.0 to 200 $g.m^{-2}$ in 1978. When converted to metric tons per hectare per year these figures, 0.01 to 1.99 t. $ha^{-1}.yr^{-1}$, compare favourably with ranges of net primary production stated by Lieth (1973) for tundra dwarf shrubs and open desert shrub communities (1-4 t. ha^{-1}. yr^{-1} and 0.1-2.5 t. $ha^{-1}.yr^{-1}$, respectively). The contribution of roots to Hudsonia net production was not determined, and therefore, an adjustment upward is necessary. Given the root to shoot ratio and the general lack of observed new roots in soil profiles, the adjustment may be minor. Significant variations within the Blowout and Dune sites were found for net annual production. The Hudsonia-lichen and the Hudsonia strongly depositional sand communities had significantly greater amounts of net annual production, 124 to 199 $g.m^{-2}$. This similarity was due to a significantly greater amount and number of shoots in relation to previous years' growth in the sand community and a significantly greater amount of previous years' growth in the lichen community. At the Dune transect, significant differences in shoot growth for meters 55 and 60 were due to significantly greater amounts of previous years' growth and not greater amounts or numbers of shoot growth per amount of previous years' growth (Fig. 12).

Significant variations between years and between sites in the net annual production and allocation on a per plant basis were found between 1977 and 1979 at the Blowout (Table 16). The length of the study was too short to clearly determine the cause of these variations. However, it appears that 1978 was an exceptional year in that approximately 50% of growth was allocated to reproduction. If reproductive growth was mathematically reduced to similar levels as in 1977 and 1979, then net annual production, number of vegetative shoots and, reproductive and net annual production per amount of previous years' growth were similar to 1977 and 1979 levels. These data would then fit into an overall pattern of consecutive increase in these parameters with increasing shrub age.

The reason for high allocation to reproductive growth in 1978 is unclear. The involvement of an endogenous rhythm or cycle of seed production is unknown. Weather conditions did vary between the three years of the study and exceptional conditions occurred. In 1977, May was hot and and wet, August was cold and September dry. In 1978, September was wet and in 1979, July was hot. The overall growth-season summary indicates that 1976 and 1977 were warmer and wetter, 1978 was slightly cooler and slightly drier and 1979 was warmer and drier than NORMS (Table 3). As most reproductive buds are formed the preceding year, the warm and wet preceding two years may have had some influence on the number of reproductive buds formed for 1978. The relatively cooler and drier summer of 1978 did not limit vegetative growth relative to other years.

The unusually high (15.8) ratio of net annual production per amount of previous years' growth in 1977 may relate to excessive sand burial in late 1976 and early 1977 before the initial readings of previous years' growth were taken. Or, it may relate to significant overwintering losses of previous years' growth. Differences in the amount of net annual production in the preceding year and the amount of last year growth in the current measurement year indicate a loss of 4.6×10^{-3} and 16.4×10^{-3}g. plant^{-1} or 25% from 1977 to 1978 and 35% from 1978 to 1979 respectively (Table 16). Evidence of leaf and whole branch abscission was noted in spring, possibly due to wind and ice caused abscission. The amount of previous years' and last year growth were not measured at the start of the 1979 growth season. Only in sand deposition sites was this of concern as last year growth was easily determined by its coloration in August of 1979. In depositional sites the position on the lowest branch was recorded as the height of sand burial at the start of the season.

Variations in growth and carbon allocation between sites indicated that the *Hudsonia*-strongly depositional sand community was significantly different from other communities (Table 16). The significantly greater amounts of net annual production was due to a large ratio of net annual production to amount of previous years' growth. Plants in this site were more vigorous; mean total plant weight was from 83 to 206% greater than that in other sites (Table 16). Several site characteristics may be involved, especially sand burial. Depth of sand burial in this site averaged 2.16 cm and the regression of net annual production per plant (g) = 0.0422 (the amount of burial in cm)-0.0151 was significant at the 0.01 level.

Analyses from the burial experiments support the concept that moderate levels of sand deposition (as in this experiment) stimulate

Hudsonia shoot growth (Plate 8). In the 1978 experiments, sand burial increased mean length of vegetative growth per plant, and, vegetative shoot growth and net annual production per amount of previous years' growth (Table 20). The 1977 data (Table 19) were inconclusive as burial treatments occurred after the period of growth flush and were poorly maintained. In the 1978 experiments, sand burial did not significantly effect percent allocation to vegetative or reproductive shoots. As buds were predetermined the previous year, the effect of burial was on the amount of growth. However, a trend towards vegetative allocation was noted (Table 20 and Fig. 23).

Although sites other than the Hudsonia-strongly depositional sand community were statistically similar in terms of their growth and carbon allocation (Table 16), trends in variation were supported by site differences and treatment effects in the sand burial (Table 20) and lichen removal experiments (Table 22). Both lichen removal and sand burial had significant effects on Hudsonia performance. Net annual production per amount of previous years' growth was the greatest in the lichen community after sand burial (Table 20). In response to lichen removal, percent allocation to vegetative and the amount of vegetative shoot growth per amount of previous years' growth increased at the expense of reproductive shoot growth (Table 22). These data indicate that Hudsonia growth and allocation pattern was influenced by lichen presence and the absence of sand deposition (Table 21).

The multiple linear regressions reported in Table 17 provide a framework from which Hudsonia growth and percent allocation can be better understood. The equations have limited use and are meant only to display relationships. The interpretation of degree-day and total precipitation effect has to be guarded as three different sample dates were used. It is of interest to note that last year growth was negatively correlated to the amount of vegetative shoot growth per amount of previous years' growth, and that standing dead was negatively correlated to percent allocation to vegetative growth (Table 17). This hints at the possibility of cyclic patterns of vegetative growth per amount of previous years' growth, and a directional trend over time towards reproductive growth versus vegetative growth in plants with increasing amounts of standing dead. This would be the case in sites without sand deposition. Indeed, sand deposition in the Hudsonia-sand community with standing dead (Table 20, No. 2), showed a large percent allocation to vegetative growth after burial.

In summary, Hudsonia, during this study has demonstrated a large variation in aboveground net production, biomass and allocation. Variation within years and sites, and within the burial and lichen removal experiments, indicate a flexibility of response which ensures plant survival in these variable habitats. Hudsonia can not be classified as either a strict r or k-strategy plant according to the definitions of several authors (Harper and Ogden 1970, Gadgil and Solbrig 1972, Ogden 1974, Pianka 1970, and Pitelka 1977). It does display characteristics of early succession species in disturbed or unstable environments; higher reproductive to total biomass ratios, larger numbers of seeds and a low competitive ability in more stable environments. However, Hudsonia is not locked into one particular growth pattern. It is able to respond to sand burial and show significant increases in mean length of growth and net annual production, thereby avoiding density-independent mortality. Significant variation in allocation patterns related to age, ensure that reproductive growth is limited until the plant is established.

SOIL PLANT INTERACTIONS

INTRODUCTION

The importance of soil microbes in determining plant succession, and plant ability to tolerate harsh environments, such as in arid regions within the temperate zone, is often overlooked in plant ecological studies. This is due to the complexity of soil microbe interrelationships, the difficulty of making quantitative measures, the great numbers of species and their often short successional prominence.

In xeric, nutrient poor sites, such as the sand dunes and blowouts, the importance of the microflora cannot be overlooked. For example, association of mycorrhizal fungi improve plant growth and enhance revegetation especially on phosphorous deficient lands by improving nutrient uptake and mobilization of nutrients (Mosse, Hayman and Arnold, 1973, and Marks and Kozlowski, 1973). Autotrophic microbial succession by blue green and green algae often occurs before higher plant succession takes place in many arid soils of temperate regions. A succession sequence described by Booth (1941) for Kansas grasslands after abandonment or fire has the algae as the primary pioneers, followed by mosses and then seed plants. In burned heath lands of England, the first colonizers are green algae, followed by lichens and fungi, and then seedlings of heath plants (Fritsch and Salisbury, 1915). Franz and Bliss (personal comm.) have found green algae as pioneer species in the totally devasted 'soils' on Mt. St.

Helens. These algae are able to persist under extreme conditions. The influence of soil algae on sandy xeric sites include: binding of sand grains and soil particles preventing wind erosion (Chepil, 1958), runoff (Fletcher and Martin, 1948) and rain splattering (Booth, 1941); retention of moisture by higher absorption and reduced evaporation (Booth, 1941, Durrell and Shields, 1961); fixation of atmospheric nitrogen (Cameron and Fuller 1960) and retention of NH_4^+ and NO_3^- (Waksman, 1951); trapping of spores and seeds within the algal crust providing a more suitable germination environment and plant growth substances (Fogg, et al., 1973); improvement of moisture conditions for fungal growth, the mycelium of which further aid in stabilizing the sand (Bond and Harris, 1964); and, the provision of organic matter for the development of secondary heterotrophic succession and solvents for demineralizations (Martin, 1939).

In this study, a green coloration of sand grains surrounding Hudsonia was noted in the field. A preliminary examination of these grains indicated the presence of unicellular, filamentous and colonial algae. The purpose of this study was to determine the extent, and nature of this green coloration, especially in terms of N_2 fixation.

MATERIALS AND METHODS

Field and laboratory studies of nitrogen fixation were done by the acetylene (C_2H_2) reduction technique (Hardy, et al., 1971). This assay involves a measure of nitrogenase activity in moles acetylene reduced to ethylene (C_2H_4) which is then converted to moles N_2

fixed. The C_2H_4/N_2 conversion factor suggested for calculations is three, the theoretical value from electron requirements (Hardy and Holsten, 1977). Concentrations of ethylene were determined by a portable gas chromatograph designed after Mallard, et al., (1977) and constructed by University of Alberta Technical Services. This instrument makes use of a Taguchi Gas Sensor which detects the presence of combustible or oxygen reducing gases, such as C_2H_4. Filtered and regulated ambient air compressed in a clean garden sprayer was used in the field as the carrier gas. The sample was presented to the detector after passage through a 44 cm Porapak R and N column. In laboratory studies, the carrier gas was compressed air. The gas chromatograph was initially calibrated against a Hewlett-Packard Model R-2 gas chromatograph in the Microbiology Department, University of Alberta. Standards for calibration in the laboratory and field were prepared from pure ethylene and acetylene gas (Linde Speciality Gases, Edmonton, Alberta). Depending upon the flow rate, the time for the ethylene peak to emerge was 45 to 75 sec and was recorded by maximum meter needle deflection in the field or peak height on a Fisher Series 5000 Recordall in the laboratory. The acetylene peak followed in 120 to 150 sec. Calibration and flow checks were run at least once every 30 min in order to avoid excessive calibration change. A 1 ml injection size was used and at least 3 min were allowed between successive readings. The gas chromatograph power supply was a 12V lead-acid battery in the field or a Hewlett Packard-Harrison 6284A DC Power Supply in the laboratory.

Samples were collected, and treated in 50 ml Belleco culture flasks sealed with rubber serum stoppers. Care was taken to insure atmospheric pressure inside the flasks. In all cases, three control types were run: flask only, flask plus sample, and flask plus acetylene. Treatment consisted of 2.5 ml of acetylene per flask in the field and 5 ml in laboratory studies. All incubations were done under aerobic, and varying temperature and light conditions. Analyses were performed after varying lengths of time. Wet and dry weights were determined for all samples. Samples were kept and used for microbe identification and culturing. These were placed in liquid and/or plate culture media, designed for blue green algae: ASM-1 with and without nitrogen (Gorham, et al., 1964).

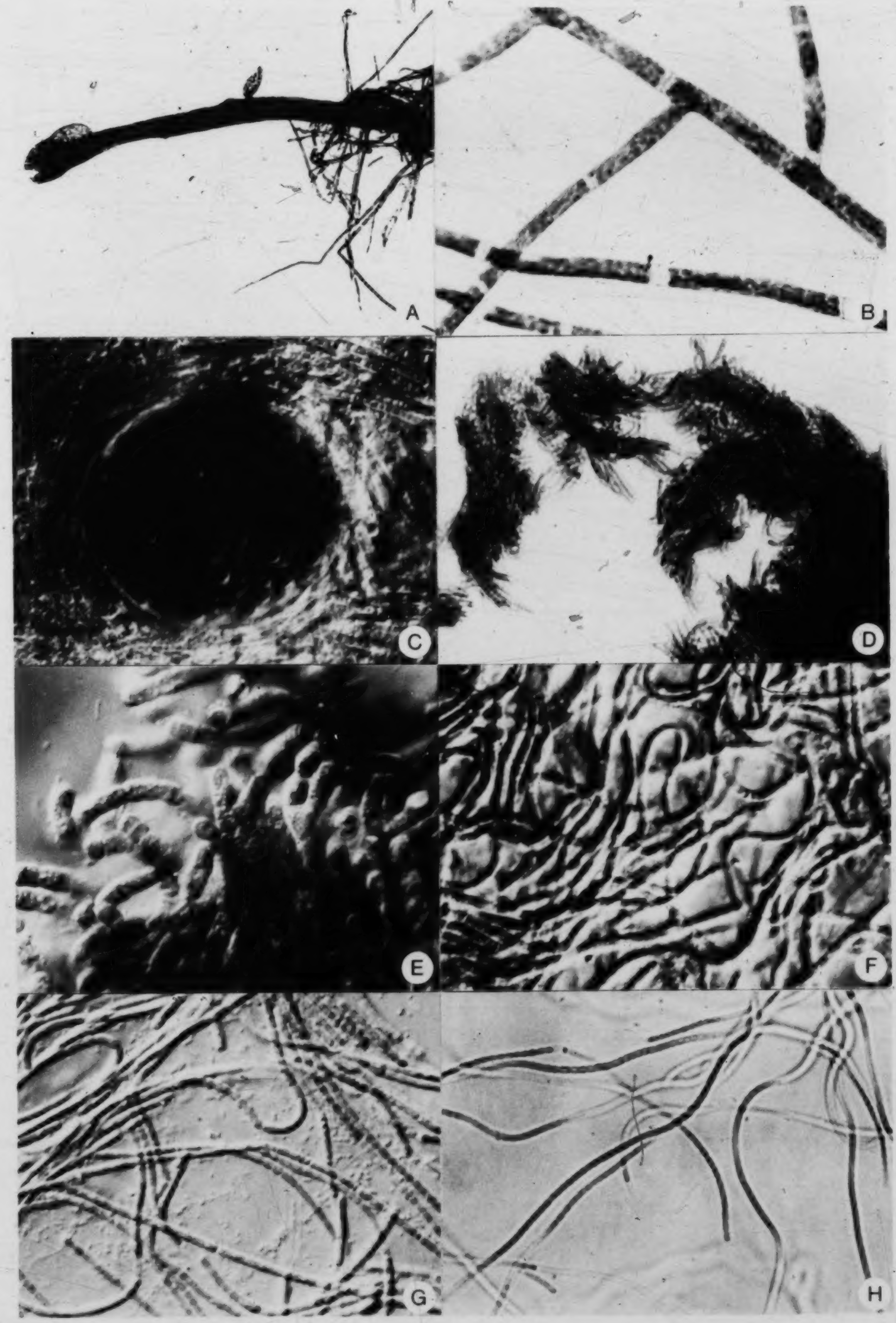
Plated species were further isolated for identification and apparently mono-species colonies placed in liquid ASM-1 culture media with and without nitrogen. These cultures were tested for N_2 fixation capacity after a 1-2 mon growth period under constant low light (75 $uE.m^{-2}.sec^{-1}$ PhAR) at 20°C. The strongest N_2 fixing cultures were recultured by placing 1 ml aliquots in fresh ASM-1 without N. These were grown for 2 wk under the same light and temperature regimes. Levels of N_2 fixation were determined for these flasks at 20°C. Flasks were flushed clear of ethylene and acetylene, and placed on a temperature bar (5 to 40°C). The temperature of each flask was monitored by a 5 mil copper constantan, thermocouple wire. Rates of N_2 fixation were determined in each flask and corrected for their relative differences at 20°C.

RESULTS

Green colored sand grains were found at several locations within both study sites. In areas of Polytrichum piliferum dominance, after wet periods, moss protonema growth was extensive and resulted in sand grain binding due to the numerous green branched filaments (Plate 9A and B). Surfical algal crusts or mats were also found in areas protected from extensive sand deposition and excessive air movement. These crusts were not developed around Hudsonia plants and were limited to wetter areas such as depressions or dune slacks at the Maybelle River Dune System.

A third and fourth type of green colored sand grains, only associated with Hudsonia were found at both study sites. These types were either within 1 cm distance of a plant part (i.e. rhizosphere, buried phyllosphere, or fallen fruit), or were located at the surface to varying depths (Fig. 18) under or downslope from Hudsonia, but more than 1 cm from any plant part (Plate 10). The latter, often occurred as distinct green bands at the sand surface extending to 50 cm below a plant. These bands were distinctly green at the surface and degraded in distinctiveness and color to shades of brown with depth (Fig. 18). Distinct green bands were still found at a depth of 22 cm. The migration of green bands into the soil was related to the movement of soil wetting fronts after period of rain. For example, the water content above and below an uppermost green band was 2.78% and 2.13% respectively, whereas the uppermost green band (15 cm below surface) was 8.23%. Similarily, green coloration of downslope sand occurred at

Plate 9 Light microscopy of moss protonema and blue green algae isolated from *Hudsonia* buried phyllosphere sand samples; developing moss shoot and protonema 218X (A), moss protonema 604X (B), *Microcystis* 604X (C), Nostacaceae-like 218X (D), Nostacaceae-like 604X (E), *Lyngbya* 604X (F), *Lyngbya* 604X (G), and *Oscillatoria* 604X (H).


A
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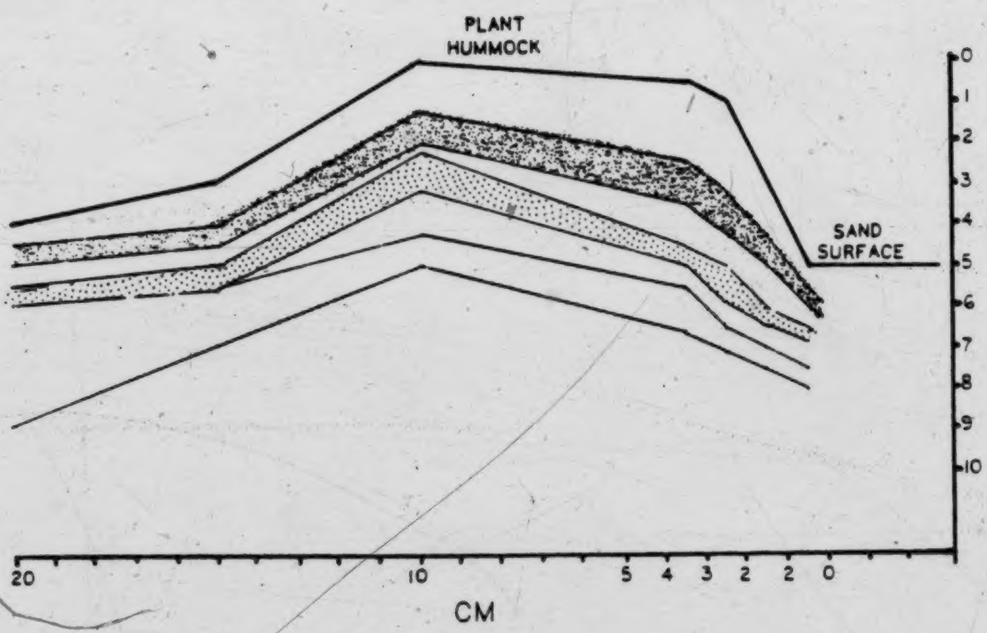


Figure 18 Location of bands of green sand below a Hudsonia plant located in a slightly depositional sand community, sampled July 30, 1978. Bands varied in coloration from distinctly green (▓) to brownish green (⁙) and to brown (░).

Plate 10 Location of green soil bands under a Hudsonia plant (A) and under a collection of fruit (B). The fruit had just been removed.

COLOURED PICTURES
Images en couleur

distances up to 60 cm from the nearest plant. The intensity of soil coloration was greatest in sites with sand deposition and was not nearly as obvious in sand deflation sites. These sand grains were not intensely colonized by algal or fungal components, but appear to have been stained by water soluble plant leachates.

Green sand grains located in the plant-sphere of Hudsonia were bound into masses which retained their shape when disturbed; unless air-dried. Microscopic examination indicated that they contained filamentous algal and fungal components. This type was most common in slightly depositional sites and was consistently in the buried phyllosphere and occasionally found associated with the rhizosphere. After rainy periods, the sand around fallen fruit became intensely green colored (Plate 18). As many as 173 distinct green spots associated with fallen fruit per m^2 were counted for a single plant (Fig. 19). These spots varied in size from 1 to 6 cm^2. This sand also contained algal and fungal components, but to a lesser degree.

Positive C_2H_2 reduction associated with either plant, lichen or moss species was only found for Hudsonia, Peltigera apathosa and Peltigera malacea (Table 27). The rhizosphere and roots of common grasses on dune ridges and the vascular plants and other lichens revegetating the western edge of the Maybelle River Dune System did not show any C_2H_2 reduction. Species located in dune slacks were not tested.

At the Blowout, the maximum C_2H_2 reduction rate observed was 4.8 nmoles $C_2H_4.g^{-1}.d^{-1}$ in 1977 and 23.9 nmoles

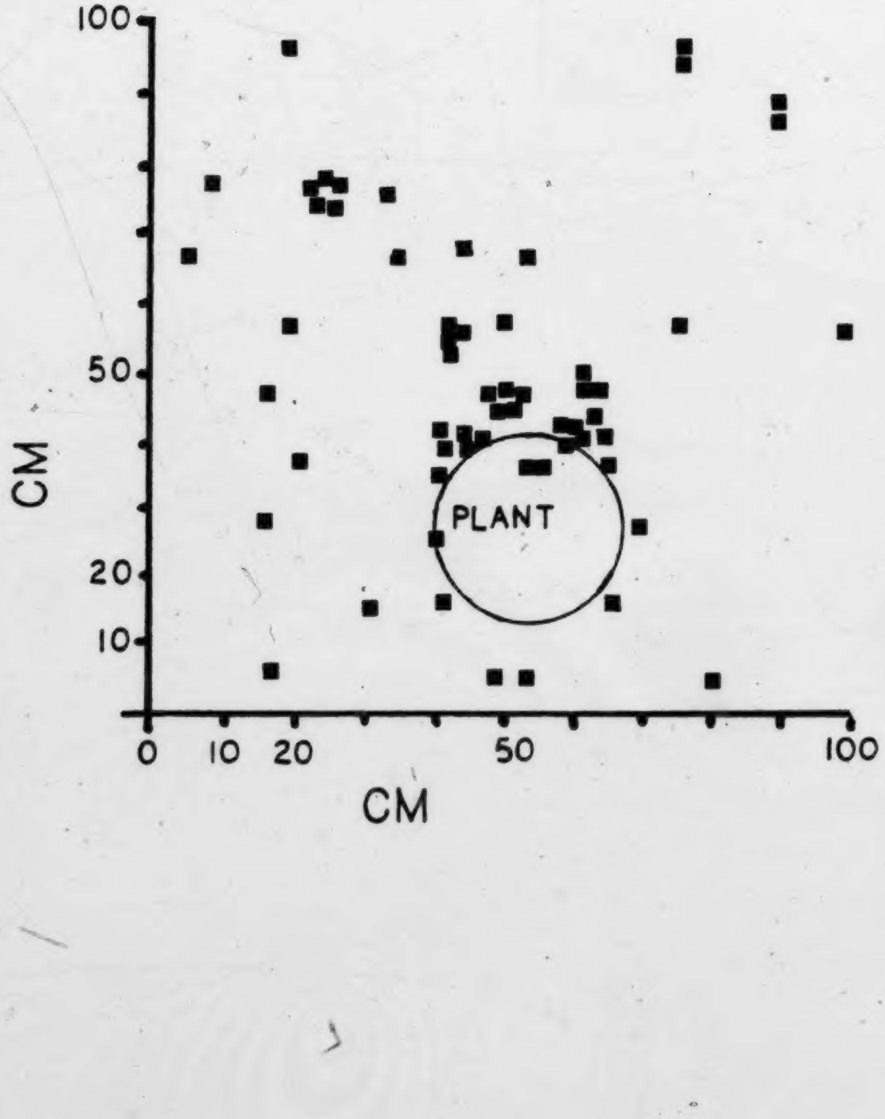


Figure 19 Representative location of green surficial sand in relation to fallen Hudsonia fruit and the parent plant. Each square (■) represents one to several fallen fruit and one distinct green spot.

Table 27. Survey of nitrogen fixation (acetylene reduction) associated with the main lichen, moss and vascular plant species inhabiting the western edge and transverse dunes of the Maybelle River Dune System. Fixation determined by the acetylene reduction technique over 48 hr under low light (75 uE.m^{-2}.s^{-1} PhAR) at 20°C, reps = 7. Each + indicates a positive fixation replicate.

Species	Relative acetylene reduction at 20°C
Lichen	
Cladonia gracilis	-
Cladonia mitis	-
Cladonia uncialis	-
Cetraria ericetorum	-
Cetraria nevalis	-
Peltigera apathosa	+++++++
Peltigera malacea	++++++
Mosses	
Polytrichum piliferium	-
Vascular plants - roots and rhizosphere sand	
Bromus pumpellianus	-
Calamagrostis inexpansa	-
Agropyron smithii	-
Agrostis scabra	-
Koeleria cristata	-
Pinus banksiana	-
Empetrum nigrum	-
Tanacetum huronense	-
Hudsonia tomentosa	++++++

$C_2H_4.g^{-1}.d^{-1}$ in 1978; both from Hudsonia rhizosphere and buried phyllosphere green sand samples (Table 28). Green sand samples had greater reduction rates than white sand samples, the latter were collected at greater than 10 cm from Hudsonia plants. Far fewer white sand samples showed positive C_2H_2 reduction (14% versus 91% for green sand). Positive C_2H_2 reduction was also associated with sand around fallen fruits, and algal crusts. The rate of C_2H_2 reduction varied both seasonally (Fig. 20) and with water content (Table 29). The greatest C_2H_2 reduction occurred in late July and early August after periods of rainy weather in both 1977 and 1978 (Fig. 20); rates in May and mid-August were reduced. Two separate experimets in which water content was varied, indicated that the maximum sample water content for C_2H_2 reduction in green rhizosphere-buried phyllosphere Hudsonia sand was approximately 30% (Table 29). Polynomial regression of C_2H_2 reduction rate (Y) versus water content (X) was $Y = 0.3226 + 0.0947X - 0.0114X^2 + 0.0005X^3 - 0.00007X^4$, $R^2 = 0.551$. Green non-rhizosphere or non-phyllosphere sand tended to have lower C_2H_2 reduction rates (Table 29).

The rate of C_2H_2 reduction was not significantly influenced by water soluble leachates from Hudsonia fruit as compared to sterile distilled water at a water content of 20% (Table 30).

Field samples showed a consistent early high reduction rate (0 - 7 hr) followed by an abrupt decline in rate (Fig. 21). Laboratory cultures showed a logarithmic increase in C_2H_2 reduction rate with time over a 48 hr period (Fig. 22).

Table 28. Nitrogen fixation (acetylene reduction) at the Blowout in 1977 and 1978; survey of various sample types within the Blowout (A) and around a single Hudsonia plant (B). In (B), mean ± 95% confidence interval separation was by the 't' test, $n = 3$. Incubation period was 24 hr at ambient temperature and light levels.

(A) Sample type	Location	Maximum rate (nmoles $C_2H_4 \cdot g^{-1} \cdot d^{-1}$)	Samples with acetylene reduction (%)
Green sand	rhizosphere and buried phyllosphere of Hudsonia	23.9	95
Green sand	beneath fallen fruit Hudsonia	16.3	83
Green sand	downslope and below Hudsonia	11.8	50
White sand	at least 10 cm from Hudsonia	2.9	14
Algal crust	slight depression	13.9	90

(B) Sample type	Location	Acetylene reduction (nmoles $C_2H_4 \cdot g^{-1} \cdot d^{-1}$)
Green sand	rhizosphere and buried phyllosphere	4.79 ± 0.73 a
Green sand	below plant in band	3.48 ± 1.10 a
White sand	50 cm from plant	0.05 ± 0.13 b

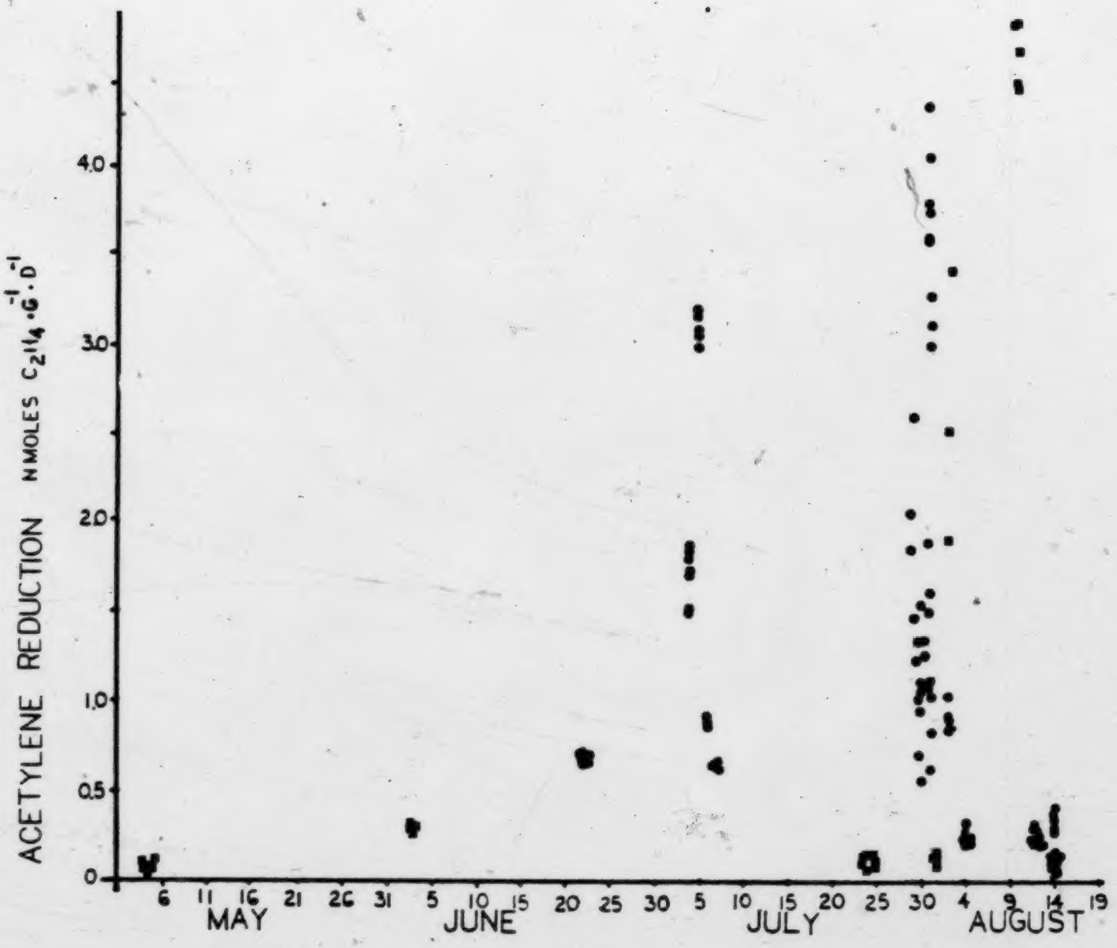


Figure 20 Seasonal variation in nitrogen fixation (acetylene reduction) for green rhizosphere and buried phyllosphere sand surrounding Hudsonia. Sample water content, temperature and length of incubation varied between measures, ■ = 1977, ● = 1978. Maximum rate of fixation in 1978 was 23.9 nmoles $C_2H_4 \cdot g^{-1} \cdot d^{-1}$.

Table 29. Influence of sand type and water content on nitrogen fixation (acetylene reduction) of sand surrounding Hudsonia. ANOVA, mean ± 95% confidence interval separation within a row by Duncan's Multiple Range Test at 0.05 level, reps = 4. In A , soil types were green sand from Hudsonia rhizosphere and buried phyllosphere (1) and green sand from band beneath Hudsonia plant but not in rhizosphere or buried phyllosphere (2). Water content was 1.4% (1), 9.1% (2) and 15.3% (3). In B , soil type was green sand from Hudsonia rhizosphere and buried phyllosphere, and water content was 2.50% (1), 10.0% (2), 22.0% (3), 28.0% (4) and 40.0% (5).

Mean rate of acetylene reduction (nmoles $C_2H_4 \cdot g^{-1} \cdot d^{-1}$)

Experiment A

Sand type		Water content		
1	2	1	2	3
0.56±0.18 a	0.35±0.13 b	0.17±0.18 b	0.58±0.13 a	0.58±0.11 a

Experiment B

Water content				
1	2	3	4	5
0.47±0.30 bc	0.56±0.47 abc	0.60±0.21 ab	0.79±0.37 a	0.33±0.04 c

Table 30. Influence of sand type and water soluble Hudsonia leachate on nitrogen fixation (acetylene reduction) of sand surrounding Hudsonia. ANOVA, mean-separation within a row by Duncan's Multiple Range Test, 0.05 level. Sand type 1 was green sand in rhizosphere and buried phyllosphere of Hudsonia and 2 was green sand below Hudsonia but not in rhizosphere or buried phyllosphere. Water supplement type 1 was water soluble leachate from fallen fruit of Hudsonia and 2 was sterilized distilled water. The same samples were measured at two different dates, August 2, 1978 and August 14, 1978, reps = 9. Water content was 20% after addition of 3 ml of either distilled water or leachate.

	Rate of acetylene reduction (nmoles $C_2H_4 \cdot g^{-1} \cdot d^{-1}$)			
Date	(a) Sand type		(b) Water supplement	
	1	2	1	2
Aug. 2, 1978 after 12 hr incubation	0.92 a	0.65 b	0.68 a	0.89 a
Aug. 14, 1978 after 12 hr incubation	0.14 a	0.09 a	0.11 a	0.13 a

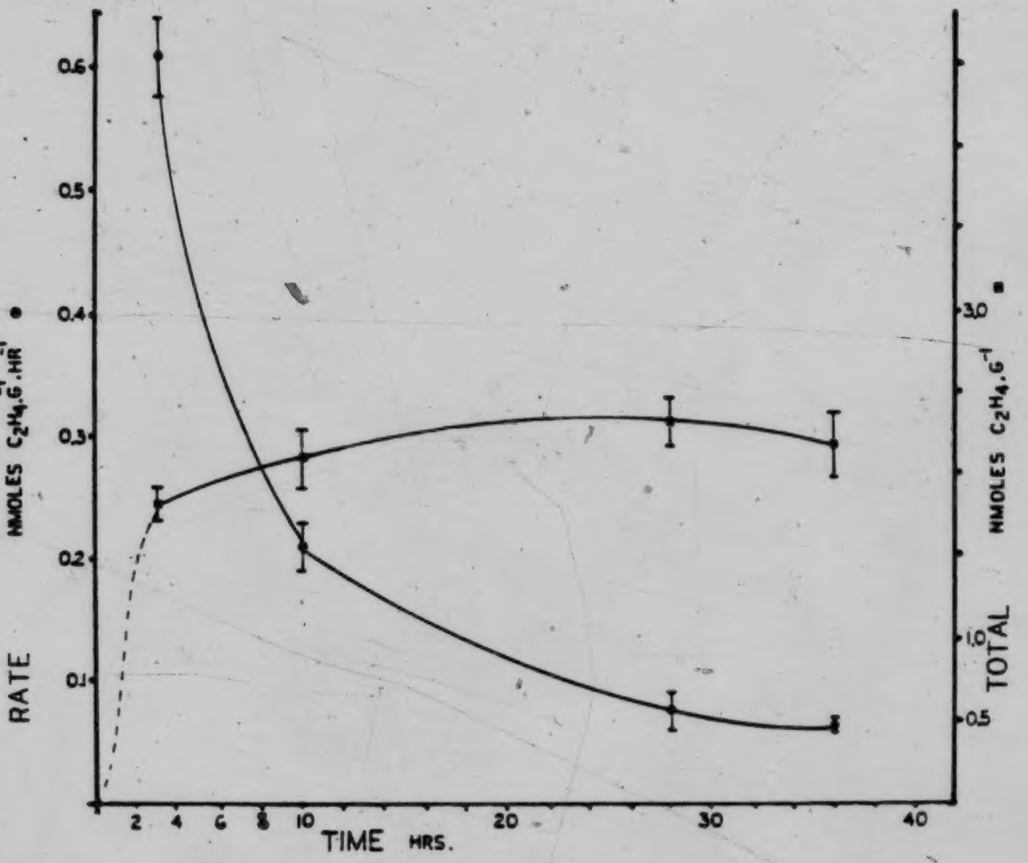


Figure 21 Time course of rate (●) and total (■) nitrogen fixation (acetylene reduction) for green soil around fallen *Hudsonia* fruit after heavy rain. Samples collected July 29 and treated at 0830 July 30, 1978. Values are mean ± 95% confidence interval, n=6.

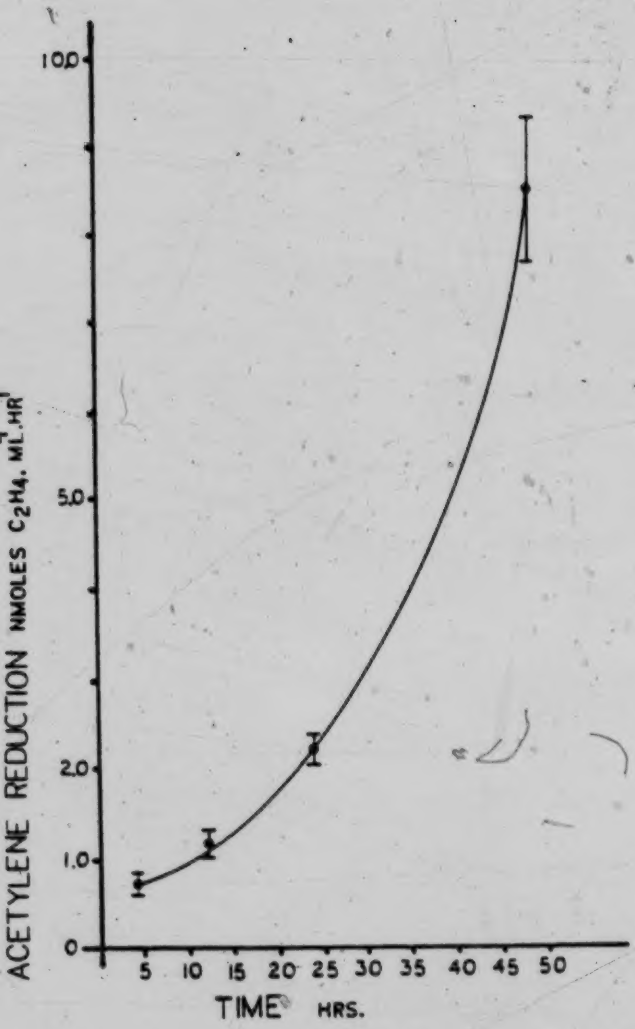


Figure 22 Time course of nitrogen fixation (acetylene reduction) rate for blue green algal cultures in liquid ASM-1 without N. Values are mean ± 95% confidence interval of 12 cultures grown for two weeks. The curve is a fitted linear regression, $\ln Y = -0.5375 + 0.0557X$, $r_{xy} = 0.9998$, $n=48$.

Isolation of microbes on ASM-1 N-free media, from field samples which had positive C_2H_2 reduction, indicated the possible involvement of Oscillatoria, Lyngbya, and Nostacaceae-type filamentous, and non-filamentous Microcystis blue green algae (Plate 9 and Table 31). Samples contained varying amounts of these blue greens, with the occasional sample contaminated by gram (-) bacteria (at least 2 types) and green algae (several circular and colonial types). More bacteria occurred on these plates than on FUM-1, a 0_2 indicating media for culture of Spirillium N_2 fixing bacteria (personal comm. Dr. Cook, Plant Science Department, University of Alberta). Another media AZO, designed for isolation of N_2 fixing Azotobacter did not yield positive results. Spirillium was isolated on FUM-1 from some of these cultures, however, when tested for C_2H_2 reduction, only one culture was active. Contaminated plates or colonies were avoided when reculturing. Recultures from plates in liquid ASM-1 without N showed positive C_2H_2 reduction at rates much greater than field rates. The presence of N in the media, reduced C_2H_2 reduction significantly regardless of the N status of the culture origin (Table 32). The highest reduction rates were associated with samples containing predominately Oscillatoria, Lyngbya and/or Nostacaceae-type and a lower number of Microcystis. However, as all samples contained a mix of these blue greens it was not clear if any one of them was a dominant C_2H_2 reducer. Recultured samples did not contain a noticeable bacterial or green algae component. The temperature optima for C_2H_2 reduction of blue

Table 31. Blue green algae isolated from positive nitrogen fixing samples of the rhizosphere and buried phyllosphere of Hudsonia. Samples isolated in ASM-1 minus N.

Species	Plate	Description	Cell diameter or width(u)	Cell length(u)	Colony diameter(u)	Frequency of occurrence
A. Filamentous						
Oscillatoria-type	9 H	filaments single or interwoven; trichomes unbranched, cylindrical non-tapering and without a perceptible sheath; heterocyst lacking;reproduction by hormogones.	2-4	6	>200	high
Lyngbya-type	9 F,G	filaments single or interwoven, either straight or twisted; trichomes unbranched, cylindrical non-tapering, rounded apices and a firm distinct thin sheath enclosing a single trichome and often projecting beyound apices; heterocysts lacking;reproduction by hormogones.	2-4	3-7	>200	high
Nostocaceae-like	9 D,E	filaments shoot and massed together; trichomes simple, unbranched, non-tapering and form into a many trichomed colony; very blue green in color, heterocysts apparent.	5	5	40-80	moderate to high
B. Non-filamentous						
Microcystis	9 C	many celled colony spherical to variably shaped, cells spherical and densely aggregated within colonial envelope, very blue green color.	4-6	4-6	60-200	moderate
Merismopedia		many celled flat colony with cells regularily arranged in a recti-linear series, cells hemispherical.	2-4	2-4	15-20	rare

Table 32. Influence of N on nitrogen fixation rate of blue green algal cultures. Rates were determined after 30 d culture from field samples (a) and after 30 d reculture (b). Mean ± 95% confidence interval, n = 7 for both (a) and (b). In (a) 't' analysis, in (b) ANOVA with mean separation within rows by Duncan's Multiple Range Test at 0.05 level. Incubation period was 48 hr at 20°C and low light (75 uE.m^{-2}.s^{-1} PhAR).

	Rate of acetylene reduction (nmoles C_2H_4.ml culture^{-1}.d^{-1})			
Origin of sample	ASM-1 with N	ASM-1 without N	t	df
(a)				
Green buried phyllosphere sand of Hudsonia	7.38±2.69	1007.31±426.35	-5.11	12
(b)				
ASM-1 with N	7.30±1.50 a	1012.45±460.82 b		
ASM-1 without N	8.58±0.54 a	880.46±500.47 b		

green algae cultures was in the high 20's to low 30's °C; described by polynomial regression $Y = 2.881 + 0.838X - 0.079X^2 + 0.0039X^3 - 0.0006X^4$ (Fig. 23). Death of cultures at 40°C occurred after attempted regrowth at 20°C.

DISCUSSION

A complete study of the role soil microbes play in the revegetation of dune and blowouts was not made. It had previously been determined, that Hudsonia was infected mostly by Cenococcum and 'other' mycorrhizal fungi at Richardson Fire Tower hill and a nearby burn site (Danielson in Bliss and Mayo, 1980). Although not identified, black hyphal mantles somewhat similar to those of Pisolithus tinctorius and short mycorrhizal-like roots were observed on Hudsonia at both study sites. These were observed more frequently at non-depositional or deflational sites in partially lichenized areas. Hyphal extensions were observed in the green sand associated with Hudsonia rhizosphere and especially the buried phyllosphere. The presence of endomycorrhizae was not determined by Danielson, or in this study. The significance of these associations remains undetermined. However, in nutrient poor and potentially droughty environments, a significant role for mycorrhizal associations has been shown and they are likely to be important here as well.

The only vascular plant at the study sites which had detectable levels of N_2 fixation associated with it was Hudsonia (Table 27). A complete survey was not performed and it is likely that other

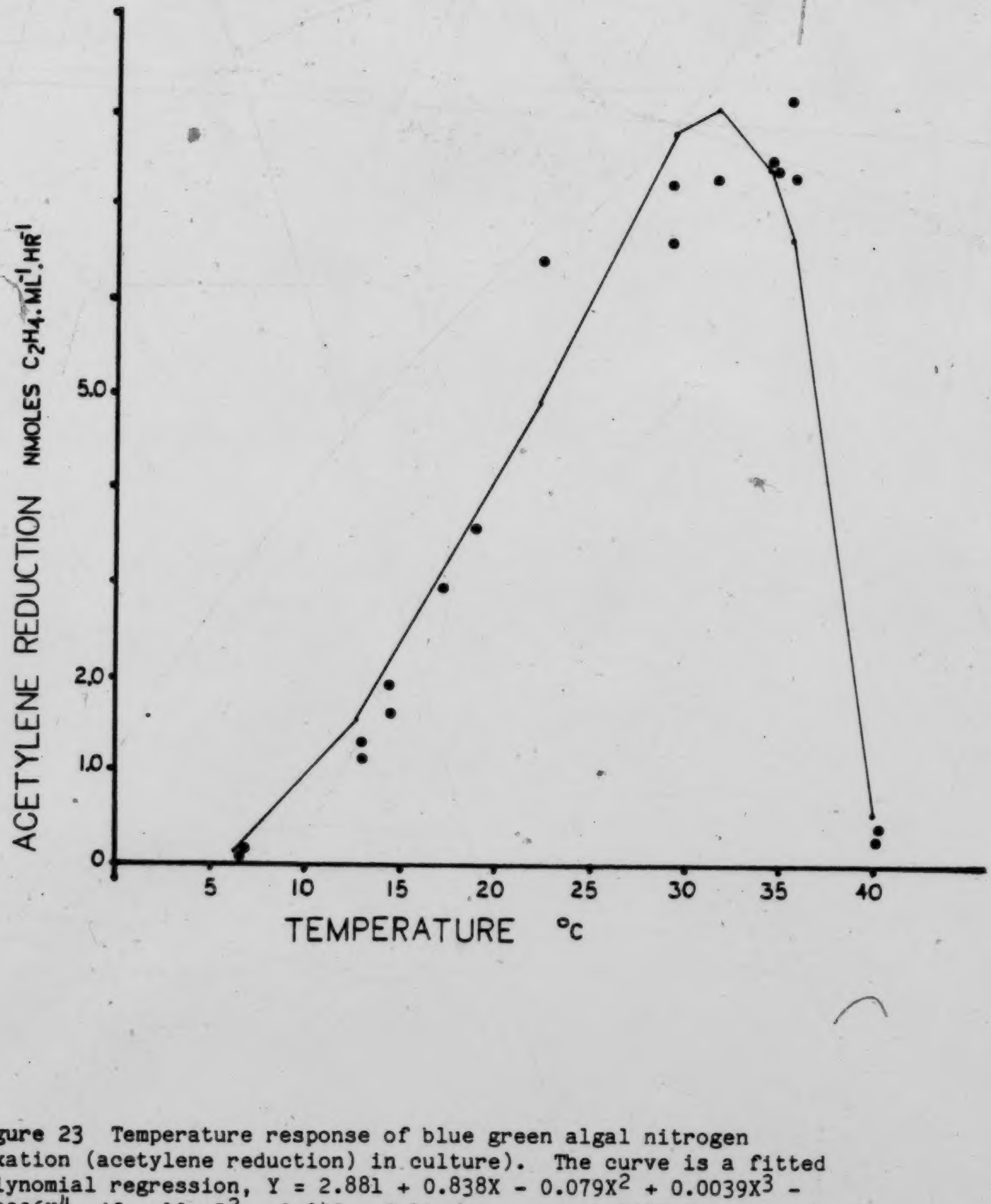


Figure 23 Temperature response of blue green algal nitrogen fixation (acetylene reduction) in culture). The curve is a fitted polynomial regression, $Y = 2.881 + 0.838X - 0.079X^2 + 0.0039X^3 - 0.0006X^4$, df = 13, $R^2 = 0.940$. Cultures grown at 20°C for two weeks in ASM-1 without N and final rate of fixation measured at 24 hr after acetylene injection.

N_2-fixing species could be found in the *Pinus*-lichen woodlands. For example, *Myrica* species (Becking 1977) and *Alnus* species (Becking 1977) have been shown to contain nodule bearing and/or N_2 fixing rhizospheres in other ecosystems. Also, *Arctostaphylos uva-ursi* has been shown to fix N_2 (Allen, et al., 1964) however contradicting data exists. Nodules associated with *Arctostaphylos* in this region are probably due to nematodes and any N_2 fixation associated with *Arctostaphylos* is rhizospheric (J. Mayo, personal comm.). N_2 fixation in *Peltigera*-lichens agrees with previous reports (Millbank and Kershaw, 1970). In this case a *Nostoc* blue green algae was responsible for N_2 fixation.

Green sand coloration associated with *Hudsonia* consists mostly of an algal component in the rhizosphere or buried phyllosphere, and/or a plant leachate component at varying locations around and under the plant. Both were most visible after rainy periods; the rain improving soil moisture levels, and washing the aboveground plant parts. Plant leachates moved through the soil as distinct bands associated with the movement of wetting fronts. The chemical nature and influence of these plant leachates was not determined. It was probable that these leachates influenced soil microbe numbers and selection by providing carbohydrates, mineral nutrients and an altered C/N ratio. It was unclear whether or not these leachates functioned as allelopathic compounds on vascular plants, as the lack of any significant co-habitat for *Hudsonia* precluded this evaluation. Similarily, it was unclear if these leachates influenced blue green algae selection and growth. Examples of vascular plant and blue green algae symbiosis are known; for example, Gunnera species and Nostoc punctiforme (Schaede, 1951). However, when leachates were applied to green sand from the buried phyllosphere, they did not alter C_2H_2 reduction levels within a 2 wk period (Table 30). Laboratory studies in which N was present or absent in culture media, indicate a feedback inhibition of nitrogenase activity in the presence of a NO_3-N source (Table 32). Fogg (1952) showed that NO_3-N inhibition of nitrogenese was significant but not as complete as NH_4-N in blue green algae liquid culture. The leachates could contain high N levels and, therefore, may have functioned to decrease nitrogenase activity. Unfortunately, spectophotometer sensitivity to unstable frequency output from an electrical generator in the field precluded spectrophotometric determinations of algal population size changes due to this treatment.

Variable levels of C_2H_2 reduction in Hudsonia field samples relate to the influence of temperature, light and soil water on the growth of blue green algae, and N_2 fixation. Optimal temperature for growth of blue green algae was found to be 30-35°C in many cases (Allen and Stainer, 1968). Although, temperature optima for N_2 fixation of some arctic blue greens, such as Nostoc containing Nephroma and Solorina lichens, is 15°C, the rate of N_2 fixation generally increases with temperature and has a much higher temperature optima (Stewart, 1977). Reported Q_{10} values for nitrogenase activity for cultures of Anabaene cylindrica and Nostoc commune vary from 4 to 6 (Fogg and Than-Tun, 1960, and Fogg and Stewart, 1968).

Early and late season temperatures fall below such optimal temperatures. Mid-summer temperatures at soil surface are much closer to growth and N_2 fixation optima as indicated by the C_2H_2 reduction temperature response curve of liquid blue green algal cultures isolated from field samples (Fig. 23). Stewart (1977) quotes 80 to 100% soil moisture (dry weight basis) as an optimal soil water content for N_2 fixation by blue green algae in a variety of soil types. In sands such a these, optimal fixation occurred at 30% soil moisture (Table 29), a content well above field capacity. Clearly low soil moisture limits blue green algal growth and N_2 fixation in these sands. The higher water content of the rhizosphere and buried phyllosphere provide improved opportunities for growth and N_2 fixation. Jurgensen and Davey (1968) determined the variation in population size of N_2 fixing blue green algae with increasing depth in forest and nursery soils. They found a significant drop in light, population size and N_2 fixation with depths below 2.0 cm. In these relatively translucent sands, light penetration may not be as limiting a factor for growth and N_2 fixation as temperature or soil moisture and is less likely to be involved in seasonal variations. Vlassak, et al. (1973) found that N_2 fixation in Canadian grasslands was mainly limited by temperature in spring and fall, and soil moisture in the summer.

Several factors may have contributed to the decreasing rate of C_2H_4 formation and accumulation with time in the field samples (Fig. 21). The C_2H_2 was not rigorously purified to avoid toxic affects of CO_2, acetone, SO_2, PH_3 and H_2S impurities as recommended by Hardy and Holsten (1977). Yoshida and Ancajas (1971) have shown that C_2H_4 disappearance takes place in non-sterile samples of Oryza N_2 fixing systems, presumably due to a C_2H_4 metabolizing bacteria. Similarily, Henriksson (1971) and Paul et al. (1971) detected ethylene disappearance in beach sand and prairie grassland samples, respectively. The presence of C_2H_4 metabolizing bacteria was not determined in field samples. Another potential explanation of apparent rate decrease with time was that care was not taken to seal over holes in the septa after each puncture in order to prevent leaks. However, similar numbers of punctures in laboratory studies did not prevent a logarithmic rate change.

Several studies have been performed on rhizosphere and phyllosphere non-aquatic systems and are summarized by Knowles (1977) and Mague (1977). Maximum rates of N_2 fixation measured by the C_2H_2 reduction technique were between 30 and 40 nmoles C_2H_4.g soil^{-1}.hr^{-1} for waterlogged rice paddy soils (Weinhard, et al., 1971). Maximum rates of 0.995 nmoles C_2H_4.g soil^{-1}.hr^{-1} for Hudsonia rhizosphere and buried phyllosphere sand (Table 28) are considerably lower than this. They are more comparable to rates of 0.04-0.8, 0.001 and 1.5 nmoles C_2H_4.g soil^{-1}.hr^{-1} which were reported for Glyceria rhizomes (Bristow, 1974), Ammophilia roots and rhizosphere sand (Hassouna and Wareing, 1964) and Saccharum rhizosphere (Dobereiner, et al., 1972), respectively.

Relatively low rates of C_2H_2 reduction in field samples under near optimal soil water contents and suitable temperatures may relate to light levels. As a function of time, light levels varied in these field samples. Initially, samples were in the light, followed by alternating dark and light periods. Considerable evidence indicates that the rate of N_2 fixation in blue green algae is controlled by the available carbohydrate pool (Lex, et al., 1972). Although dark heterotrophic growth and N_2 fixation by blue green algae is possible at low rates for 1 to 24 hr (Khoja and Whitton, 1972), it is likely that dark rates were reduced and therefore reduced overall rates on a time basis.

It has been shown (Yoshida and Ancajas, 1971) that some systems require greater C_2H_2 levels than that used in this study and normally used in other studies; 0.05 atm (Yoshida and Ancajas, 1973). This was not tested.

Definitive proof and identification of blue green algal nitrogen fixation in field samples was not obtained. Bacterial contamination on plates was noted. However, apparently clean recultures maintained C_2H_2 reduction. If bacterial C_2H_2 reduction was significant, leachates could have resulted in enhanced bacterial C_2H_2 reduction, due to improved energy supply, however, this was not the case (Table 30). As these were ground plant leachates, it is not known if inhibitors were released. The fact that Azotobacter was not and Spirillium was isolated from samples is significant. However, the extent of Spirillium presence in samples and subsequent C_2H_2

reducing capacity after isolation was limited. It remains to be determined which blue green algae were reducing C_2H_2. Oscillatoria and Lyngbya species have been shown to fix N_2 in pure culture (Kenyon, et al., 1972) and appear to have been selected for on N free media in this study. The environment of the study sites is far more favorable to the autotrophic growth of blue green algae than to heterotrophic bacterial growth and may preclude significant Spirillium populations.

The relationship between blue green algae and Hudsonia in the rhizosphere and buried phyllosphere is likely to be one of protocooperation as both partners benefit, but the relationship is not obligatory. The buried phyllosphere provides an improved soil moisture environment as it soaks up water after rainfall and becomes moist most nights from dew condensation. The blue green algae, provide NH_4^+ via N_2 fixation, bind sand particles, improve water absorption and retention characteristics due to sheath materials, absorb mineral nutrients from plant leachates to prevent their loss from the system and may provide growth promotor substances (Fogg et al., 1973). Stewart (1977) suggests that higher fixation rates by blue greens when in the rhizosphere of Suaeda maritimam, Argostis stolonifera, Byrum pendulum (Stewart, 1967) and Artemesia species (Mayland and MacIntosh, 1966) may in part be explained by bacterial O_2 depletion, CO_2 enrichment and absorption of NH_4^+-nitrogenase inhibitor. Thus, in this system, an important role for bacteria, in terms of blue green algae N_2 fixation, may also be indicated.

PHYSIOLOGICAL AUTECOLOGY

INTRODUCTION

An important component in the interpretation of Hudsonia's autecology is the consideration of Hudsonia's plant water relations. Several recent reviews of plant adaptation and response to water stress have been written. Arnon (1975), Slavik (1974), Kramer (1980), Levitt (1972) and Turner (1977) review methods and point out confusing terminologies. In this study, drought refers to a meteorological and environmental event, such as the absence of rainfall, which produces plant water stress. Plant water stress refers to a variable level of plant water deficit which results from a less than optimal plant water balance (rate of water absorption-rate of transpiration). The three categories of plant resistance to drought include: drought escape, drought tolerance at high water potentials, and drought tolerance at low water potentials (May and Milthorpe, 1962). Mechanisms of drought escape include phenologic and developmental plasticity so that the drought periods are either avoided during the life cycle or development is strongly altered so as to avoid unsuitable conditions. Examples are the germination and rapid completion of the life cycle in desert ephemerals during precipitation pulses, and the avoidance of late season drought periods by early maturing wheat varieties.

Drought tolerance at low water potentials can occur either as morphological or physiological modifications which reduce transpirational water loss or maintain water uptake. Stomatal closure in response to leaf water potential varies from -0.8 to 2.80 MPa in a variety of crop plants, and is also known to vary with leaf age, growth conditions, and stress history of the plant (Turner and Begg, 1978). In many species, stomatal closure appears to occur at a 'threshold' leaf water potential. This 'threshold' concept may be an artifact associated with the use of the term resistance, as the relationship between conductance and leaf water potential is linear (Gardner, 1973 and McCree, 1974). Also, it has been shown that stomata in some species can respond directly to vapor pressure deficit. Resistance increases as vapor pressure deficit increases (Schulze et al., 1972, Camacho-B et al., 1974, and Sheriff and Kaye, 1977). This increase in resistance may be due to increased cuticular transpiration (either peristomatal or epidermal) resulting in the development of variable epidermal water deficits causing stomatal closure (Sheriff and Meidner, 1974 and Hall et al., 1976). Cuticular resistance to water loss is known to increase many species with prolonged water stress due to the deposition of cuticular substances (Blum, 1975). Increased leaf pubescence (Ehleringer et al., 1976) and leaf roll or parahelionastic movements (Begg and Torssell, 1974, and Begg and Turner, 1976) have been shown to reduce radiation absorption and leaf temperature, thereby reducing water loss (Quarrie and Jones, 1977). Reduction in leaf area and abscission of plant parts also reduce water loss (Orshan, 1963, Evenari et al., 1974, Constable and Hearn, 1978, and Ludlow, 1975). Plants in droughty environments often have high root-to-shoot ratios (Caldwell, 1976, and Fischer and

Turner, 1978) which are known to increase with increasing levels of water stress (Turner and Begg, 1978). In some species, this is due to an absolute increase in root biomass (Hsiao and Acevedo, 1974). The pattern and depth of root growth can vary depending on local soil conditions and, thereby influence drought tolerance (Turner, 1977). Resistance to water flow between roots and shoots varies between species and with environmental factors (Bunce, 1978 and Burch et al., 1978). Boyer (1971) and Kramer (1969) conclude that the major resistance within the plant occurs in the roots, however, significant resistances may also occur in stems and leaves (Dimond, 1966, Begg and Turner, 1970).

At low water potentials, another category of drought tolerance is recognized. It varies with the kind of plant, duration of stress, and stage of development as summarized by Hsiao (1973) and Begg and Turner (1976). This usually refers to cellular modifications relating to the degree of dehydration under which maintenance of growth, development and production or survival occur. The physiological basis for differences in survival of dehydration stress among species has been chiefly correlated to molecular events in membrane structure and enzymatic activity (Vieria de Silva, 1976, and Lee-Stadelmann and Stadelmann, 1976), cytoplasmic protein alteration (Sullivan and Easter, 1974), and the role of accumulating sugar for protection of the RNA-DNA complex (Parker, 1968). The extent and degree of tolerance are subject to acclimatization and hardening processes. Maintenance of growth, development and production requires the maintenance of turgor for cellular expansion (Green et al., 1971, Boyer, 1970 and Hsiao et al., 1976), operation of the stomatal aperture (Turner, 1974, and Meidner and Edwards, 1975) and activity of certain enzymatic reactions (Hsiao, 1973). Turgor can be maintained by osmotic adjustment in response to development of plant water deficit (Jones and Turner, 1978). In this case, solutes (free amino acids, sugars, K^+, Cl^-) accumulate and result in varying amounts of change in osmotic potential, and therefore, turgor maintenance. The level depends upon the rate and level of deficit (Jones et al., 1979), sensitivity of various plant parts and processes (Morgan, 1980), several environmental factors such as temperature and light (Johnson, 1978, Turner and Long, 1978), and the species or cultivar (Redmann, 1976, Morgan, 1977 and 1980). Osmotic adjustments have been shown to occur on a diurnal basis (Turner, 1975). They are transient in nature in that they disappear upon loss of deficit and may not contribute to adjustment in subsequent stress cycles (Jones and Rawson, 1979). However, a series of moderate stress cycles can result in a greater degree of adjustment in subsequent cycles or influence stomatal responses to water potential (Brown et al., 1976, Thomas et al., 1976). In addition to turgor maintenance via osmotic adjustment, there is evidence to suggest that an increase in tissue elasticity in response to water deficit can function to maintain turgor (Weatherly, 1970).

These field water relations studies on Hudsonia were undertaken in order to determine its adaptations to drought which allow it to maintain growth and survive in sandy environments.

MATERIALS AND METHODS

Tissue water relations were studied on a seasonal and diurnal basis employing several techniques. In all cases, sample height above the ground, and lengths of current, last year and previous years' tissue were recorded. Water relations were studied at the Blowout site in 1977 and 1978, and at the Dune site in 1979.

Xylem water potentials were measured with a 'Scholander pressure chamber' (PMS Instruments Co., Corvallis, Oregon) according to techniques suggested by Ritchie and Hinckley (1975). Pressure was applied at a rate of 0.05 MPa.sec^{-1}. The effect of time lapse since excision of the sample on the reading was highly variable. For example, xylem tensions measured within one minute of excision were significantly smaller and less variable than those measured on samples stored in a humidified vial over a 10 min period (0.53 ± 0.07 and 1.17 ± 0.25 MPa, respectively). For this reason, all samples were measured within 45 sec of excision, except where extremely high xylem tensions delayed endpoint determination. The amount of stem protruding from the top of the pressure chamber varied from 2 to 4 mm (measured from the rubber stopper). A PMS insertion tool was used to insert the samples into the rubber stopper, and the amount of tissue extending into the chamber varied from 5 to 8 mm as a result of seasonal variation in size of sample types. For any one measurement period, similar sample sizes were used whenever possible. In all cases, three separate values were recorded for each xylem tension determination.

Endpoint determinations were recorded when water appeared across the entire surface of the cut twig. In many cases at pressures lower than the endpoint, water came to the surface in distinct positions. The first occurrence and any secondary occurrences were recorded along with the endpoint. Bubbling and blowing dry of these areas were noted before the endpoint.

A ventilated, lithium-chloride type porometer, designed after Gresham, et al., (1975), was used to determine the resistance of twigs to diffusive water loss. In this case, the porometer was constructed of teflon and a plexiglass window inserted into the sample chamber. This window was necessary to ensure that the chamber received light, that air mixing was complete and to ensure that the inserted tissue was not bent or resting against the chamber walls. The instrument was calibrated by two methods. Tubes with various numbers of holes were filled with wicking connected to a distilled water supply and inserted into the chamber. In the second and most frequently used method, plates with varying numbers of holes were screwed onto the end of the sample chamber so that the entire area of the plate was exposed to the chamber. The plates were connected to a constant water supply. In both cases, the chamber was dried down with air pumped through silica-gel to a particular reading on a Lambda Diffusive Resistance Meter, Model LI-60. The amount of time for change of meter reading between two points on the meter (proportional to sensor wetness) was recorded. Plate resistance was calculated as follows:

$R = 4A\ (Lo + \pi\ d/4)/\alpha\ n\ \pi d^2$, where

R = resistance of plate to water loss, sec.cm^{-1}

A = area of plate, 1.2272 cm^2

Lo = length of a hole in the plate, 0.1295 cm

d = diameter of a hole in the plate, 0.0991 cm

α = diffusivity of water at calibration temperature and barometric pressure, e.g. 0.235 cm^2.sec.$^{-1}$

Change of time from plant tissue samples were processed through a regression equation derived from plate calibration, e.g. R = -3.797 + 0.6017 Temp + 0.2512 Time, n=34, multiple r_{xy} = 0.970. Tissue area was calculated from regression of tissue length and tissue area determined by the glass bead technique of Thompson and Layton (1971). Regressions were determined for different tissue types. Resistance of tissue to water loss was calculated by multiplying R times the area of tissue. The tissue was inserted into the sample chamber after the excised surface was placed into Terostat. The terostat was used to seal over the chamber. Similar sample lengths were used whenever possible, however, these varied from 10 to 20 mm depending upon seasonal and tissue type variations. The average of two to three consecutive readings was used.

Spanner-type thermocouple psychrometers, designed after Mayo (1974), were used to determine water potential and a combined osmotic and matric potential. Unless otherwise stated, samples containing 3 to 4 mm sections of the most apical stem and leaf tissue were excised and immediately placed into the psychrometer chamber. After 3 to 4 hr equilibration in a temperature monitored water bath, a 4 mAMP cooling current was applied to the psychrometer for 30 sec, and the amplified output read on a Wescor Psychrometric Microvoltmeter MJ-55. Combined osmotic and matric potential was determined in a similar manner after the sample was frozen in liquid propane (-40°C) for 30 min. The sensors were frequently calibrated against KCl solutions of known water potential.

Tissue water content was determined from fresh and dry weights determined on a Mettler HI-10 balance. Samples were transported and stored for short periods of time ($<$30 min) in humidified vials before fresh weight determination.

Net assimilation studies were carried out on transplants from the Dune sites. Plants were overwintered in cold storage after hardening off and were grown out of doors in Edmonton until flowering had taken place. Plants were then kept in a growth cabinet under the following conditions before determination of net assimilation: 16 hr light period at 24°C and 900 $uE.m^{-2}.sec^{-1}$ PhAR, and a 8 hr dark period at 17°C. Lights consisted of a mixture of lucalox and mercury multi-vapor lamps. Relative humidity varied from 53 to 76%. Plants were watered with tap water and were not fertilized. The net assimilaton measurement system was an open system, previously described by Addison (1977).

In 1978, selected plants were covered to induce drought conditions. Plants were covered prior to precipitation events in such a manner that light penetration and air circulation were not inhibited.

RESULTS

The water relations of Hudsonia were not studied between late August to late May in either of the study years. However, xylem tension of dormant but apparently healthy tissue was greater than 4.5 MPa at snow melt in 1976 (mid April at Richardson Fire Tower). Within 3 wk of snow melt, xylem tensions had declined to 0.5 MPa. Relatively small variation in xylem tension occurred from late May to late Augustin both 1977 and 1978 at the Blowout (Fig. 24). However, considerable diurnal variation and variation associated with drought development occurred (Figs. 24 and 25). The mean xylem tension for all living Hudsonia tissue types measured from May to Augustin all sites at mid-day (1000 to 1500 hr) was 1.12 ± 0.05 MPa (n=905). Mean dawn, (prior to 0800 hr) mid-morning (0800 to 1000 hr) and dusk (1700 to 2200 hr) values were 0.66 ± 0.15 (n=113), 0.99 ± 0.07 (n=588) and 0.60 ± 0.06 (n=185), respectively. Predawn values were not regularly sampled, however, those that were consistently ranged from 0.05 to 0.35 MPa.

Periods of reduced precipitation, clear skies, high temperature and high VPD resulted in an increase in daily minimum, maximum and mean mid-day xylem tension (Fig. 26). For example from June 17 to 30th, 1978, daily minimum and maximum changed from 0.05 to 0.40 MPa and from 0.53 to 1.95 MPa, respectively. Mean mid-day values changed from 0.31 ± 0.07 to 1.39 ± 0.13 MPa. Similarly from August 2 to 10, 1978, mean mid-day values changed from 0.65 ± 0.11 to 1.43 ± 0.17 MPa. High intensity precipitation events (>3 mm) were associated with decreases in mid-day dawn and dusk xylem tension and delayed the

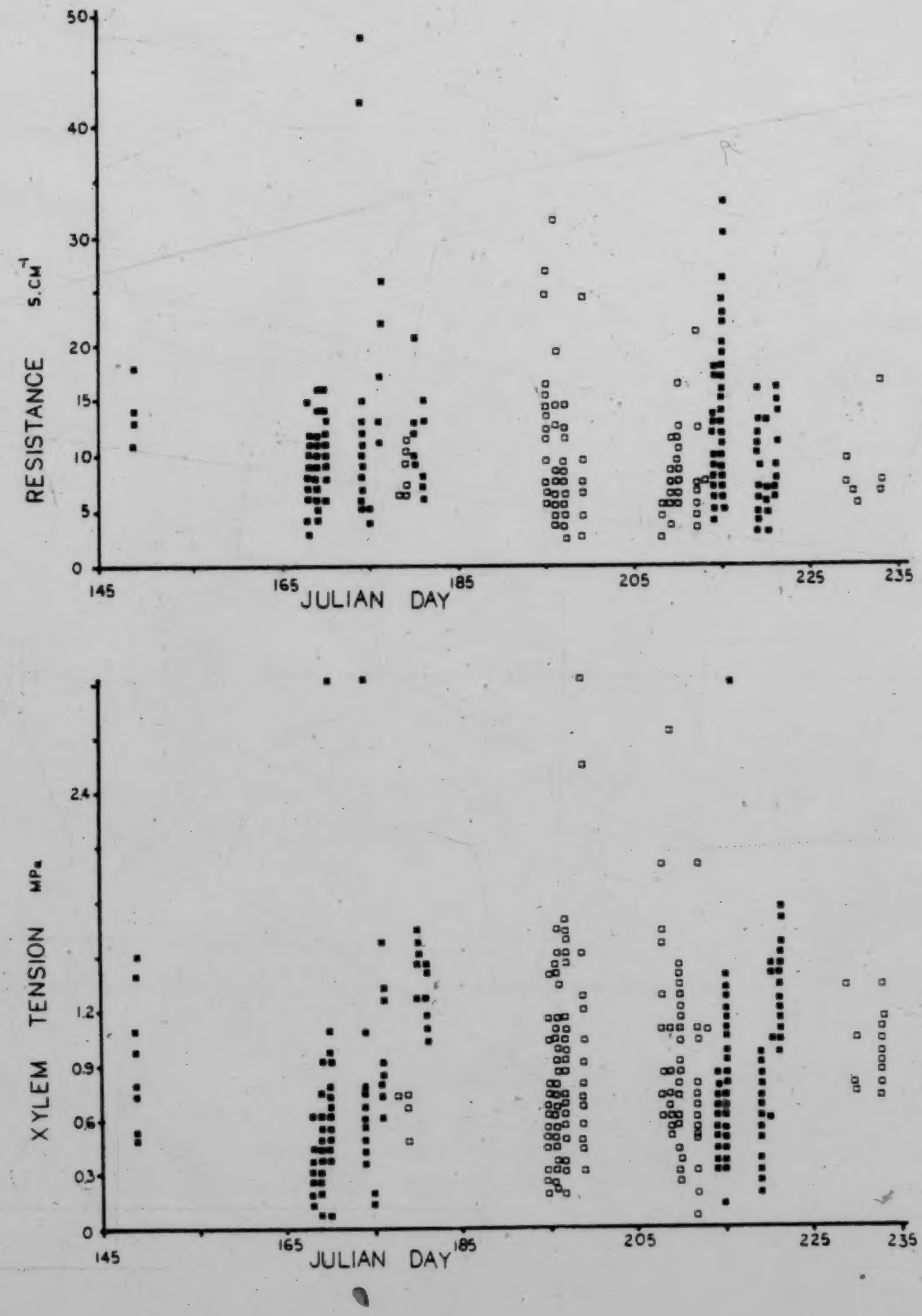


Figure 24 Variation in resistance to water loss (A) and xylem tension (B) for Hudsonia in 1977 (□) and 1978 (■) at the Blowout. Readings include all sites, dates, times and tissue types. Each plotted data value represents from one to several readings, total n=888. Xylem tensions greater than 2.0 MPa were from standing dead tissue.

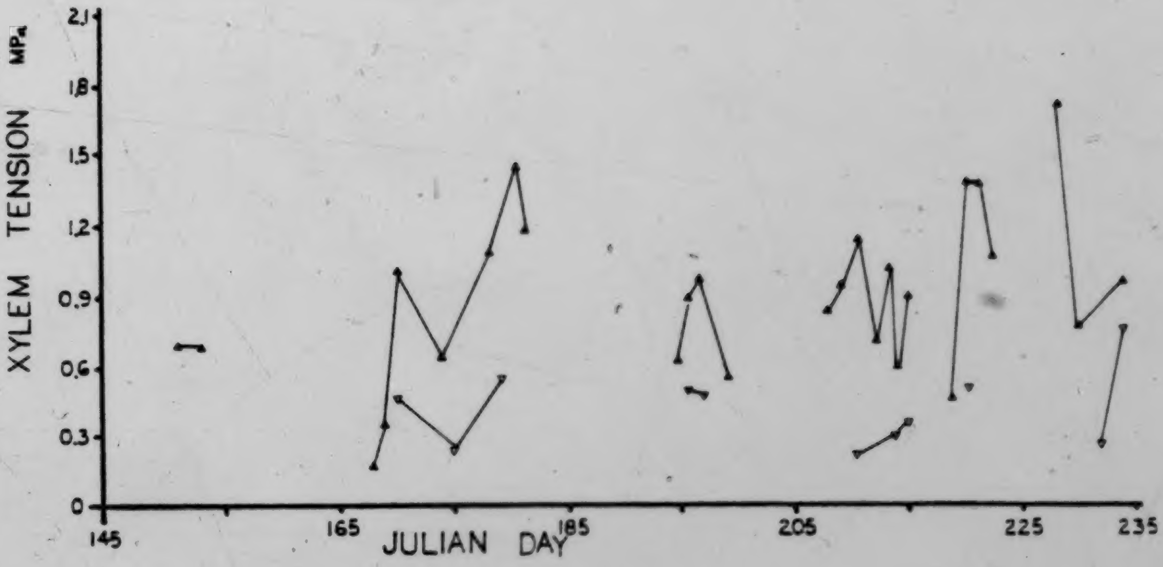
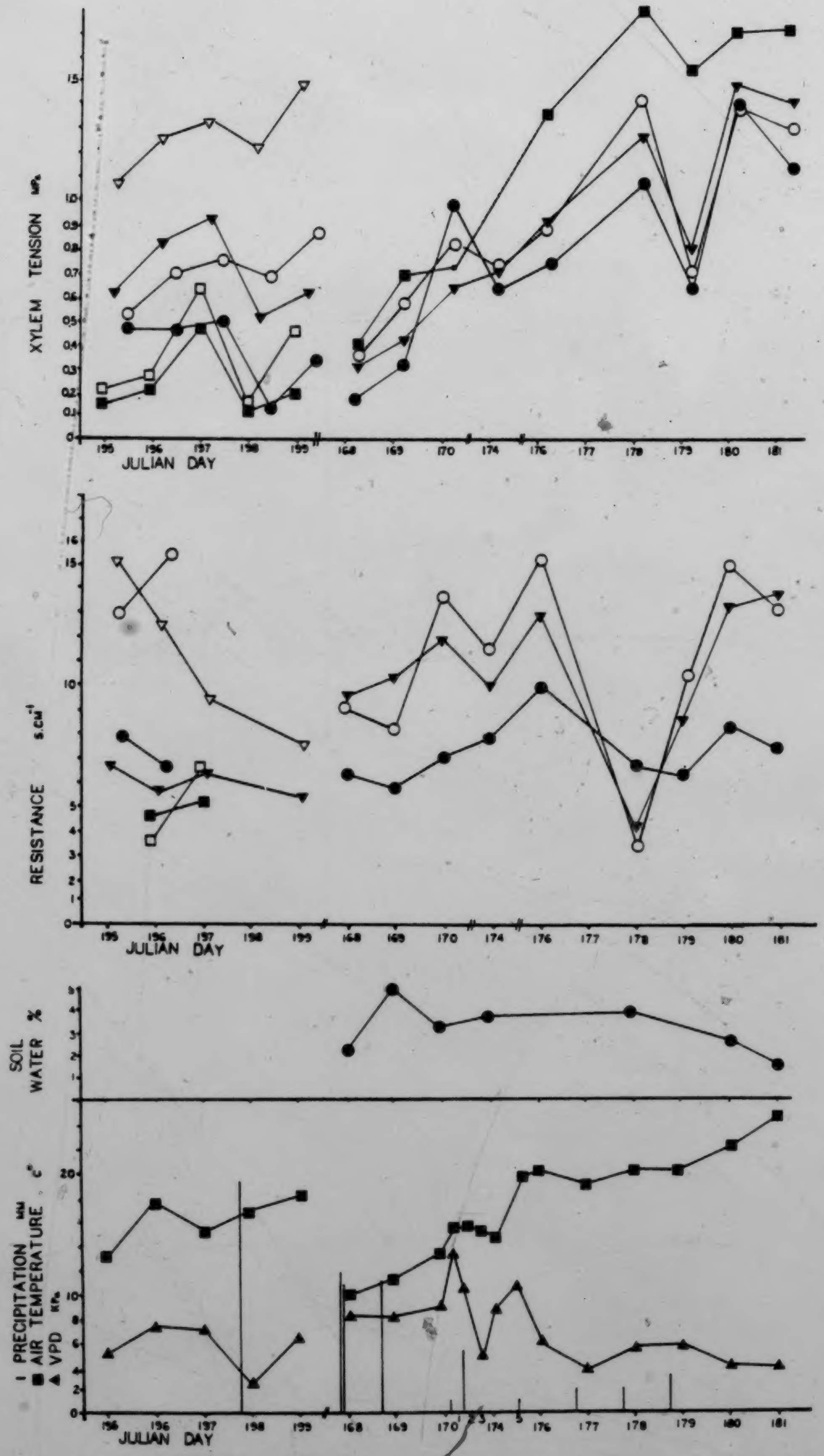


Figure 25 Seasonal course of Hudsonia mean mid-day (▲) and mean dawn (△) xylem tension for Hudsonia-depositional-sand site at the Blowout. Each plotted value is the mean of at least 7 and as many as 25 measurements over 1977 and 1978.

Figure 26 Change in environmental and Hudsonia plant water parameters. For the time period July 14 to July 18, 1977 (Julian days 195-199), the mean dawn (■, □), mid-day (▼, ▽) and dusk (●, ○) xylem tension and resistance to water loss are indicated for Hudsonia in a depositional-sand site (solid symbols) and for Hudsonia in a deflational-sand site (open symbols). For the time period June 17 to June 30 (Julian days 168-181) the mean mid-day xylem tension and resistance to water loss for Hudsonia in a lichen site (■), a deflational-sand site (▼), a depositional-sand site with (○) and without standing dead (●) are indicated. Precipitation (I), mean daily air temperature (°C) and mean daily vapor pressure deficit (VPD-KPa) are indicated.


XYLEM TENSION MPa
JULIAN DAY
RESISTANCE s.cm⁻¹
JULIAN DAY
SOIL WATER %
I PRECIPITATION mm
■ AIR TEMPERATURE C°
▲ VPD kPa
JULIAN DAY
195
196
197
198
199
168
169
170
174
176
177
178
179
180
181

development of plant water stress (Fig. 26). Evening or overnight low intensity events (<3 mm) had apparently little effect on mid-day xylem tension (Fig. 26). The influence of precipitation on xylem tension varied between tissue and site types. Mean mid-day xylem tension of tissue in a depositional-sand site was reduced in response to 5 mm precipitation, whereas, in a deflational-sand site it was slightly elevated (Fig. 26), Julian day 170 versus 174). Mean mid-day resistances also showed variability over time, however, the pattern of change appeared less predictable than xylem tension (Fig. 26).

Sudden cloud cover resulted in a rapid decrease in mid-day xylem tension (Figs. 27 and 28). A decrease of approximately 0.6 MPa was associated with a leaf temperature decrease from 31.5 to 25.3°C. Approximately 24 of the 29 days on which Hudsonia water relations were studied, had variable cloud cover during the measurement period.

Xylem tension was also found to vary with site and tissue type. Mean differences between sites or between tissues were greatest at mid-day and were reduced at dawn or dusk (e.g. Fig. 26). Statistically significant differences between site and tissue types were less obvious if values over the entire mid-day period were compared. For example, mid-day xylem tension were not significantly different at 0.85 ± 0.07 MPa (n=126) and 0.88 ± 0.07 MPa (n=136) for current year tissue and current year plus last year tissue within a deflational sand site over the entire season. Whereas, a paired 't' analysis for August2 and 3, 1978 (paired in time ± 2 min) indicated that differences were statistically significant (Table 33). However,

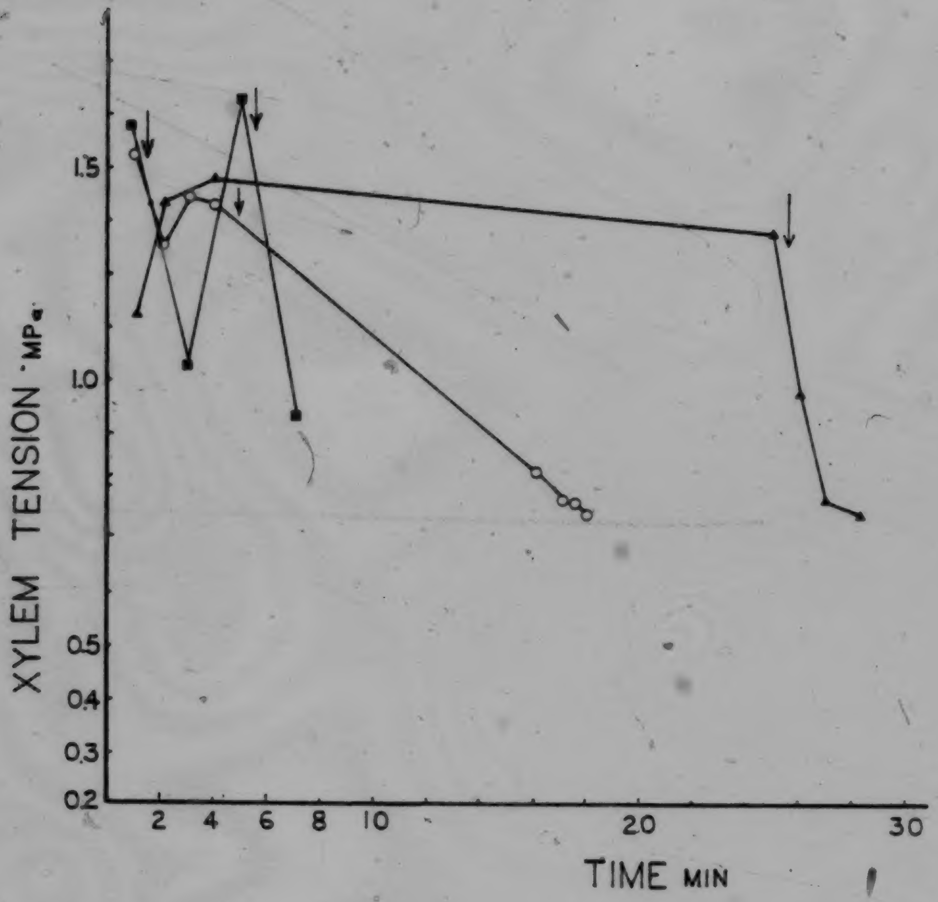


Figure 27 Influence of sudden cloud cover on Hudsonia xylem tension. Time zero (↓) in Hudsonia lichen site (○), Hudsonia-depositional-sand site (▲) and Hudsonia-deflational-sand site (■) was 1615, 1510 and 1415 hr respectively.

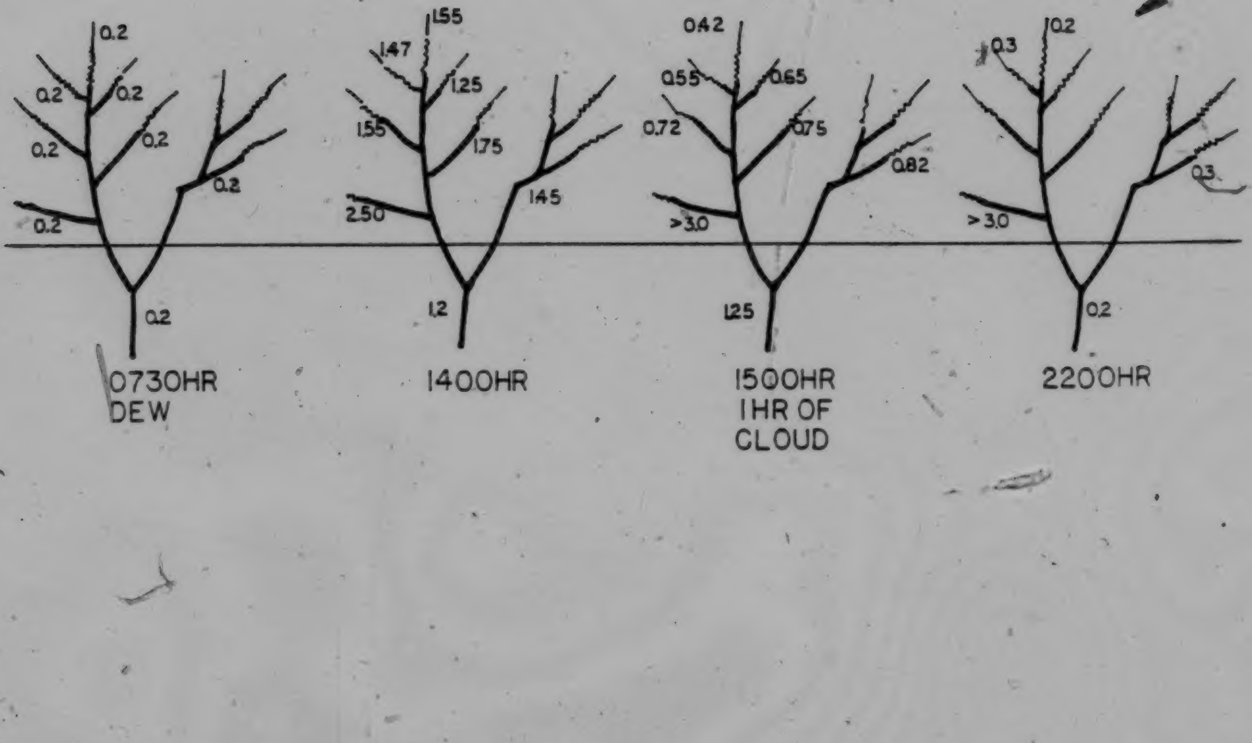

0.2
0.2
0.2
0.2
0.2
0.2
0.2
0.2
0730HR
DEW
1.55
1.47
1.25
1.55
1.75
1.45
2.50
1.2
1400HR
0.42
0.55
0.65
0.72
0.75
0.82
>3.0
1.25
1500HR
1HR OF
CLOUD
0.2
0.3
0.3
>3.0
0.2
2200HR

Figure 28 Influence of dew and cloud on diurnal change in xylem tension of various Hudsonia tissue types. Previous years' tissue (▬), last year tissue (∿∿∿), current year tissue (—) and xylem tension are indicated for the same plant sampled at various time periods.

Table 33. Influence of paired sites and tissue type analysis on mid-day *Hudsonia* xylem tension, resistance and water content, Aug 2 and 3, 1978. Data were paired within a 5 minute time period, n = 45. Analysis by paired 't' test, means within a column were separated at 0.05 level. Current year growth (VEG) and current year plus last year growth (VEG + LY) were sampled.

Site	Tissue type	Xylem tension (MPa)	Resistance ($s.cm^{-1}$)	Water content %
Hudsonia-depositional sand	VEG	0.74 b	7.58 b	95.3 b
	VEG+LY	0.73 b	16.56 a	112.5 a
Hudsonia-deflational-sand	VEG	0.59 c	--	--
	VEG+LY	0.87 a	--	--

the xylem tension of current year plus previous years' (last year plus standing dead) tissue (1.21 ± 0.07 MPa, n=139) was significantly greater than either current year (0.85 MPa) or current year plus last year (0.88 MPa) tissue, and significantly less than standing dead (3.95 ± 0.28 MPa) tissue over the entire period of measure. When analyses were performed on specific days, tissue types without last year or previous years' tissue tended to have lower xylem tensions and resistances (Fig. 26, and Tables 33 and 34). Also, Hudsonia in depositional-sand sites had lower mid-day xylem tensions (Table 33 and 34) than either deflational-sand (Fig. 26) or lichen-sites (Table 34). However for similar tissue types, over the entire period of measure, only the Hudsonia- lichen site had significantly different mid-day xylem tensions. For example, mid-day xylem tensions for current year plus last year tissue were 1.38 ± 0.31, 0.88 ± 0.06, and 0.94 ± 0.08 for the lichen, deflational and depositional sites, respectively.

Considerable variability in xylem tension was noted within plants. This was especially noticeable in plants with a lot of previous years' growth, i.e. Hudsonia-lichen or Hudsonia-deflational-sand sites. For example, xylem tensions on similar combinations of tissue types differed as much as 0.43 to 0.83 MPa 30 min after cloud cover for an individual plant (Fig. 27) or from 1.25 to 1.75 MPa at mid-day (Fig. 28). A similar pattern of variability within a plant, as depicted in Fig. 28, was found at dusk and during tissue wetting-up. A large gradient in mid-day xylem tension occurred over

Table 34. Influence of time of day, site and tissue type, and storage of samples in humidified vials on xylem tension and difference between initial and complete wetting of cut surface during xylem tension determinations of Hudsonia. In A, all sites, tissue types, and times from 1977 and 1978 were used. Mean separation by nonpair 't' test at 0.05 level. In B, only mid-day readings from June 27, 1978 were used. Mean separation by Duncan's Multiple Range Test at the 0.05 level, reps = 7. In C, the same mid-day readings were compared to samples kept in a humidified vial for 10 min prior to xylem tension determination. Current year tissue (VEG) and current year plus last year tissue (VEG+LY) are indicated.

A.

Time of day (hrs)	Xylem tension (MPa)	Difference between end point and initial wetting of cut surface (MPa)	n
Before 0800	0.68±0.09 b	0.09±0.03 b	257
0800-1700	1.11±0.04 a	0.15±0.01 a	1414
1700-2400	0.67±0.05 b	0.08±0.01 b	372

B.

Site	Tissue type	Xylem tension (MPa)	Difference between end point and initial wetting at cut surface (MPa)
Lichen	VEG+LY	1.21 ac	0.50 ac
Depositional-sand	VEG+LY	1.00 ad	0.29 ad
Strongly depositional -sand	VEG	0.53 b	0.02 b
Depositional-sand	VEG	0.63 b	0.06 b

C.

	Site			Time of reading	
Variable	Lichen	Depositional-sand	Strongly depositional-sand	Within 45s	at 10 min
Xylem tension (MPa)	1.42 a	1.31 a	0.86 b	0.91 a	1.48 b
Difference between end point and initial wetting at cut surface	0.48 a	0.37 a	0.09 b	0.27 a	0.36 b

short lengths of plant tissue on the same plant. Closeness to the water supply did not ensure lower xylem tensions. In lichen and deflational-sand sites with large amounts of previous years' tissue, current year growth was mostly apical, and therefore, further from the water supply. However, the most apical portions tended to 'wet-up' the quickest at dusk, or under cloud cover (Fig. 28). Previous years' tissue without any current year growth also varied in xylem tension (Fig. 28). Precipitation or morning dew resulted in the wetting up of this tissue, but it quickly dried out and remained dry so that mean mid-day values were 3.95 ± 0.28 MPa for all readings under 6.0 MPa. Several readings greater than 6.0 MPa were not completed on this tissue type.

The difference between xylem tension end point and the initial spotting of the cut surface varied with time of day, site type and tissue type (Table 34). This difference was significantly greater at mid-day, and on tissue with last year growth. It was significantly lower in the strongly depositional sand site. The maximum difference observed on tissue supporting current year growth was 1.35 MPa at mid-day in a deflational-sand site on current year plus previous year tissue.

Analysis of the drought experiment indicated that tissue water parameters were similar between the control and the drought application (Table 35). Great difficulty was experienced in maintaining the protective rain cover over the experimental plot and it was doubtful that the experimental condition existed. However,

Table 35. Influence of drought experiment on Hudsonia mid-day xylem tension, resistance and water content. ANOVA, mean separation by Duncan's Multiple Range Test at 0.05 levels, reps = 7. Mean daily VPD and air temperature for Aug 9, 1978 were 9.3 KPa and 22.2°C, respectively. Current year tissue (VEG) and last year tissue (LY) were sampled.

	(a) Drought		(b) Tissue-type	
Parameter	Drought	Control	VEG	VEG+LY
Xylem tension (MPa)	1.33 a	1.35 a	1.48 a	1.19 b
Resistance ($s.cm^{-1}$)	10.96 a	10.23 a	7.18 a	14.01 b
Water content (%)	90.3 a	104.5 a	88.6 a	106.1 a

tissue type differences were not consistent with those found previously in that the current year tissue had a greater xylem tension than that of current year plus last year tissue. This was probably due to the lower resistance of this tissue type which resulted in a lower water content and a higher xylem tension (Table 35).

Xylem tension was found to be significantly different between sites and between burial levels in the plant burial experiments (Table 36). These differences were noted at dawn, mid-day and dusk. Sand burial resulted in decreased dawn and mid-day xylem tensions, with the amount of decrease increasing with the amount of burial.

When data from all sites, times of day, dates and tissue types were analyzed, relationships between xylem tension, resistance and VPD were not especially clear. Xylem tension appeared to be linearly related to VPD while resistance did not show any clear linear relationship. The diurnal course of xylem tension and VPD (Fig. 29) indicated a mid-day plateau in xylem tension at 1.3 to 1.5 MPa and subsequent decline as VPD continued to increase. Xylem tension followed the diurnal pattern of VPD and varied as the amplitude of VPD varied. A plot of xylem tension and resistance against VPD for mixed tissue types on selected days from June 30 to August9, 1978, indicated that there was a linear increase in xylem tension with increasing VPD until 1.3 to 1.6 KPa VPD or 1.3 to 1.5 MPa xylem tension (Fig. 30). This relationship broke down at these thresholds and became a polynomial function as resistance became a logarithmic function of VPD. However, these mid-day plateaus and subsequent declines in xylem

Table 36. Influence of sand burial on mid-day xylem tension (MPa) of *Hudsonia*. Analyzed by ANOVA, mean separation within rows was by Duncan's Multiple Range Test at the 0.05 level, reps = 7. Burial levels were 0.003 ± 0.51 cm (1), 2.01 ± 0.57 cm (2) and 4.33 ± 1.45 (3) for *Hudsonia*-lichen (1), *Hudsonia*-deflational-sand (2) and *Hudsonia*-depositional-sand (3) sites. Data collected on current year tissue.

Time period	(a) Site 1	2	3	(b) Burial 1	2	3
Dawn	0.47 ac	0.20 b	0.40 ad	0.46 a	0.29 b	0.33 b
Mid-day	1.07 b	1.31 a	1.05 b	1.33 ac	1.14 ad	0.96 b
Dusk	0.24 b	0.28 a	0.28 a	0.31 a	0.31 a	0.18 b

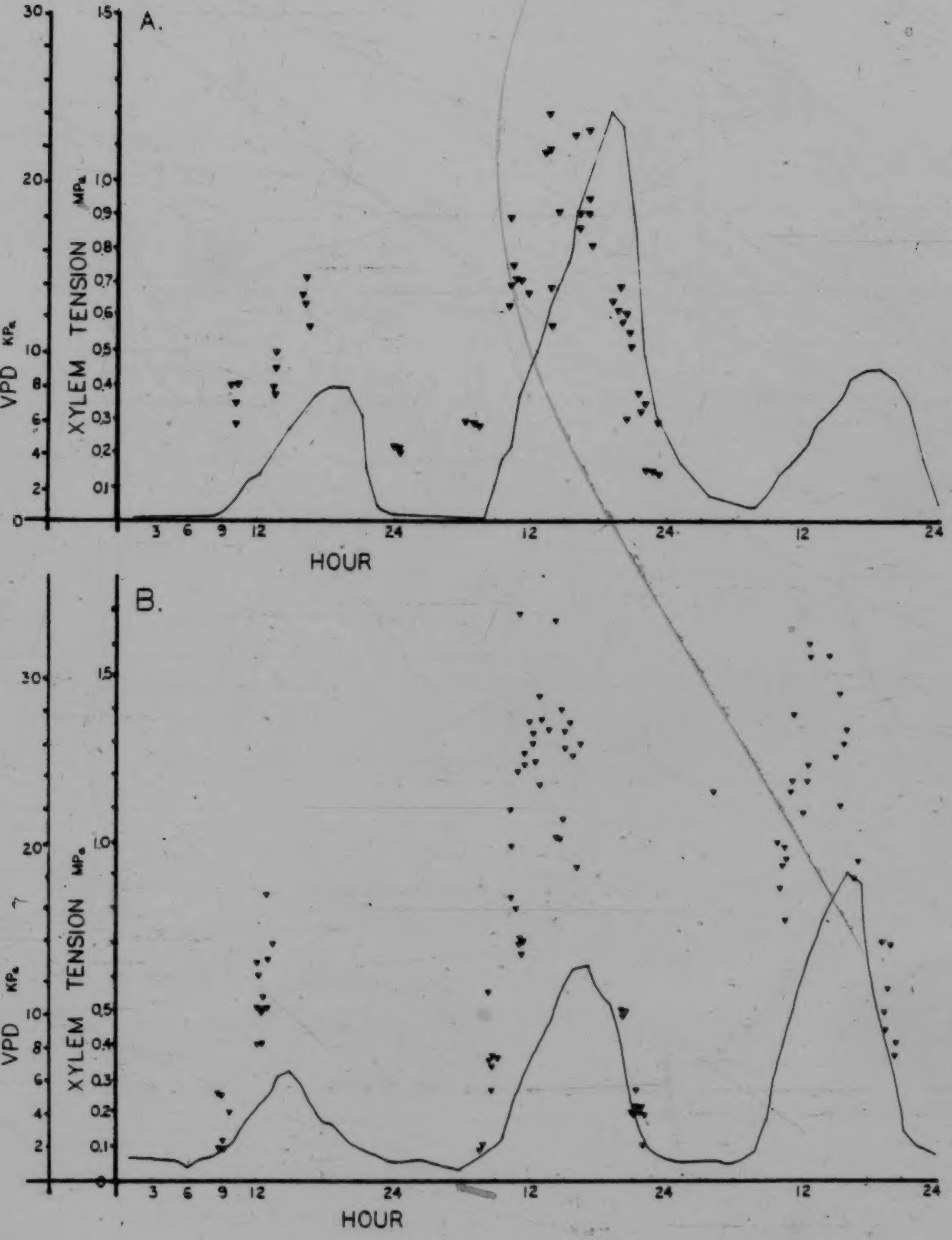


Figure 29 Diurnal course of xylem tension (▼) and vapor pressure deficit (VPD) for Hudsonia from August 2-3 (A) and August 7-9 (B) 1978. Samples were from a Hudsonia-depositional-sand site and were taken on current year tissue. Mean hourly VPD were used.

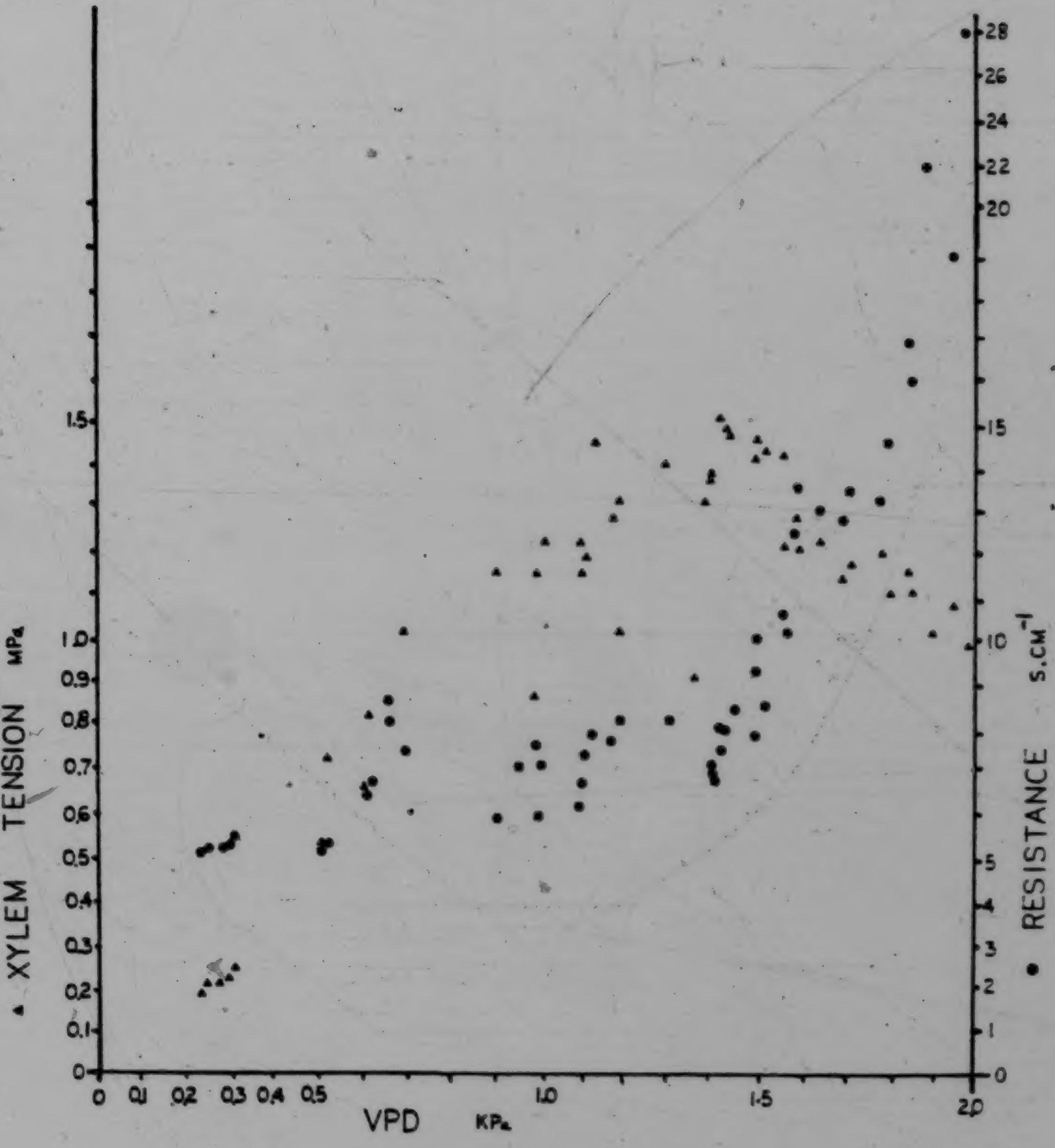


Figure 30 Influence of vapor pressure deficit (VPD) on xylem tension (▲) and resistance to water loss (●) for *Hudsonia*. Samples were taken in a *Hudsonia* sand community without standing dead during a drying spell June 30 to August 9, 1978. Current year tissue was sampled. Polynomial regression of xylem tension versus VPD, is $Y = -0.779 + 6.092X - 12.521X^2 + 14.46X^3 - 7.569X^4 + 1.411X^5$, $R^2 - 0.856$, n=47. Linear regression of leaf resistance versus VPD is $\ln Y = 1.3091 + 0.6933X$, $r_{xy} = 0.848$, n=47.

tension were often associated with periods of cloud-cover, declining radiation and reduced temperatures. For example, in Fig. 31, when data values were sequentially connected in time, the apparent breakpoint in xylem tension versus resistance coincided with clouding-up. The extent of cloud appearance during the field seasons was such that only 4 of 29 days of intensive water relations sampling were clear all day.

An analysis on those 4 days was performed on data which was matched not only in time (± 1 min) but also to the same branch of the plant. Only data between 0930 and 1730 hr were used so as to avoid low radiation. Conductance (inverse of resistance) and xylem tension showed a negative and a positive linear relationship respectively, to VPD and time of day (Fig. 32). Xylem tension plateaued at mid-day and conductance declined throughout the day. Xylem tension and conductance had a weak (correlation coefficient of 0.276, n=217) but significant relationship. The apparently small decline in conductance with time was associated with a bell shaped xylem tension response with time, however no sharp decrease in conductance or drop in xylem tension was associated with increasing VPD levels. These data were further sub-divided and differences between site and tissue types and between days were noted (Fig. 33). For example, current year tissue had a similar slope but greater conductance for a range of VPD on the same day as compared to current year plus last year tissue from the same depositional-sand site (Fig. 34).

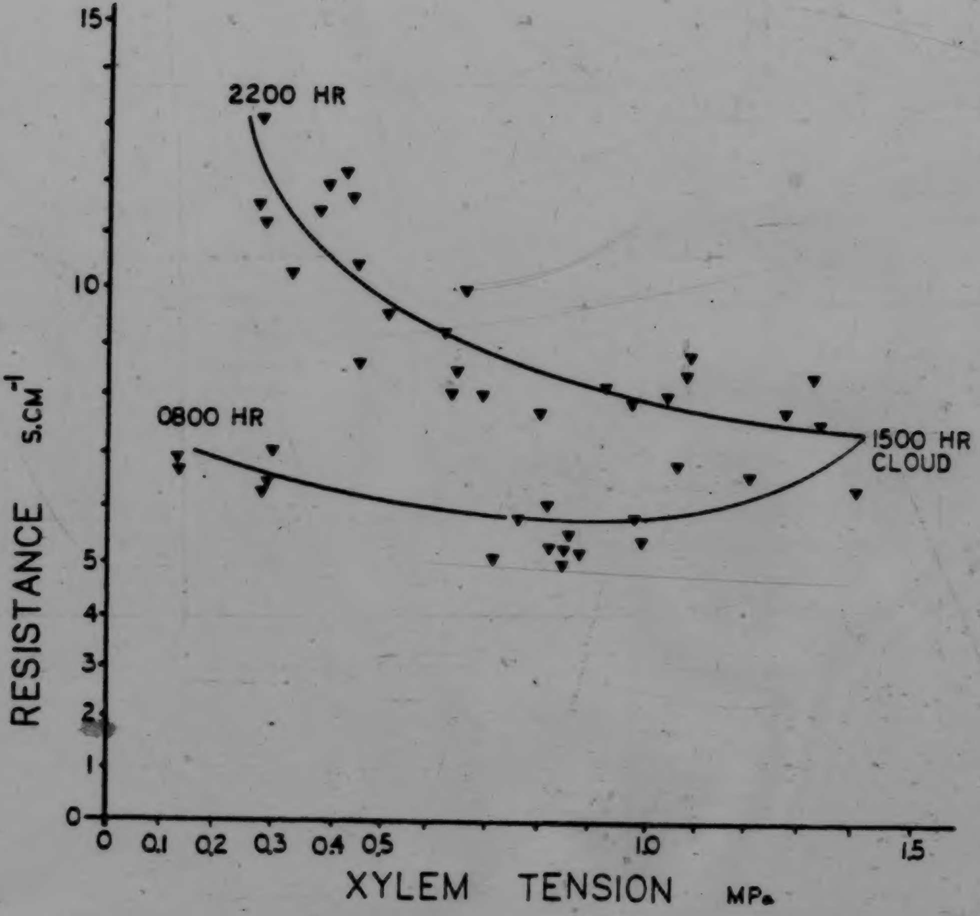
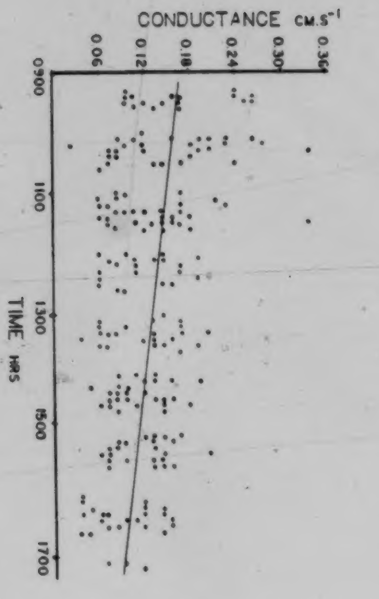
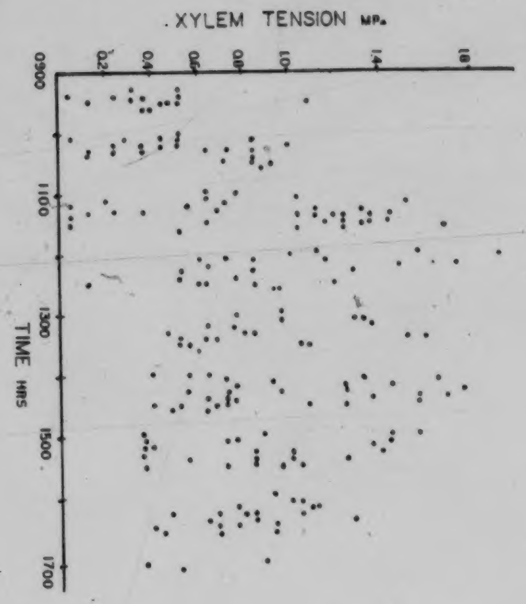
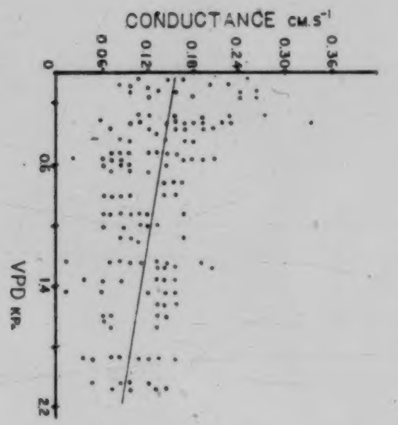


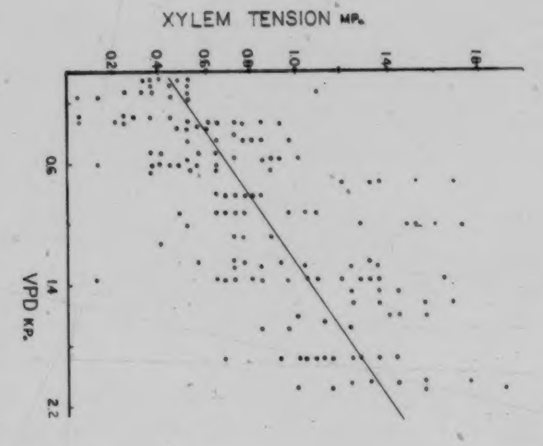
Figure 31 Relationship between xylem tension and leaf resistance to water loss over a day, August 9, 1978. Samples were from a Hudsonia-depositional-sand site and were taken on current year tissue. Samples were paired ± 2 minutes. The line represents the sequence of change with time of day.

Figure 32 Relationship of conductivity and xylem tension to time of day and VPD on 4 clear days. Days were June 29 and 30, and August 2 and 9, 1978. Regression of xylem tension versus VPD, is $Y = 0.44 + 0.42X$, $r_{xy} = 0.69$, n=217. Regression of xylem tension versus conductance, is $Y = 1.03 - 1.77X$, $r_{xy} = 0.28$, n=217. Regression of conductance versus time, is $Y = 0.25 - 0.93 \times 10^{-4}X$, $r_{xy} = -0.33$, n=217. Regression of conductance versus VPD, is $Y = 0.16 - 0.35 \times 10^{-1}X$, $r_{xy} = -0.38$, n=217.


CONDUCTANCE CM.S^{-1}
0.06
0.12
0.18
0.24
0.30
0.36
0900
1100
1300
1500
1700
TIME HRS


XYLEM TENSION MP.
0.2
0.4
0.6
0.8
1.0
1.4
1.8
0900
1100
1300
1500
1700
TIME HRS


CONDUCTANCE CM.S^{-1}
0.06
0.12
0.18
0.24
0.30
0.36
0
0.6
1.4
2.2
VPD KP.


XYLEM TENSION MP.
0.2
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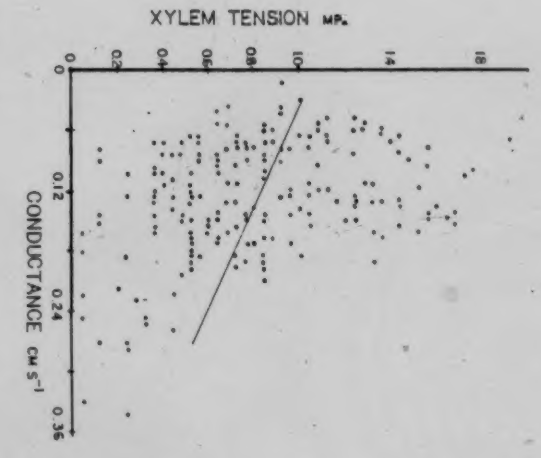
1.0
1.4
1.8
0.6
1.4
2.2
VPD KP.


XYLEM TENSION MP.
0
0.2
0.4
0.6
0.8
1.0
1.4
1.8
0
0.12
0.24
0.36
CONDUCTANCE CM.S^{-1}

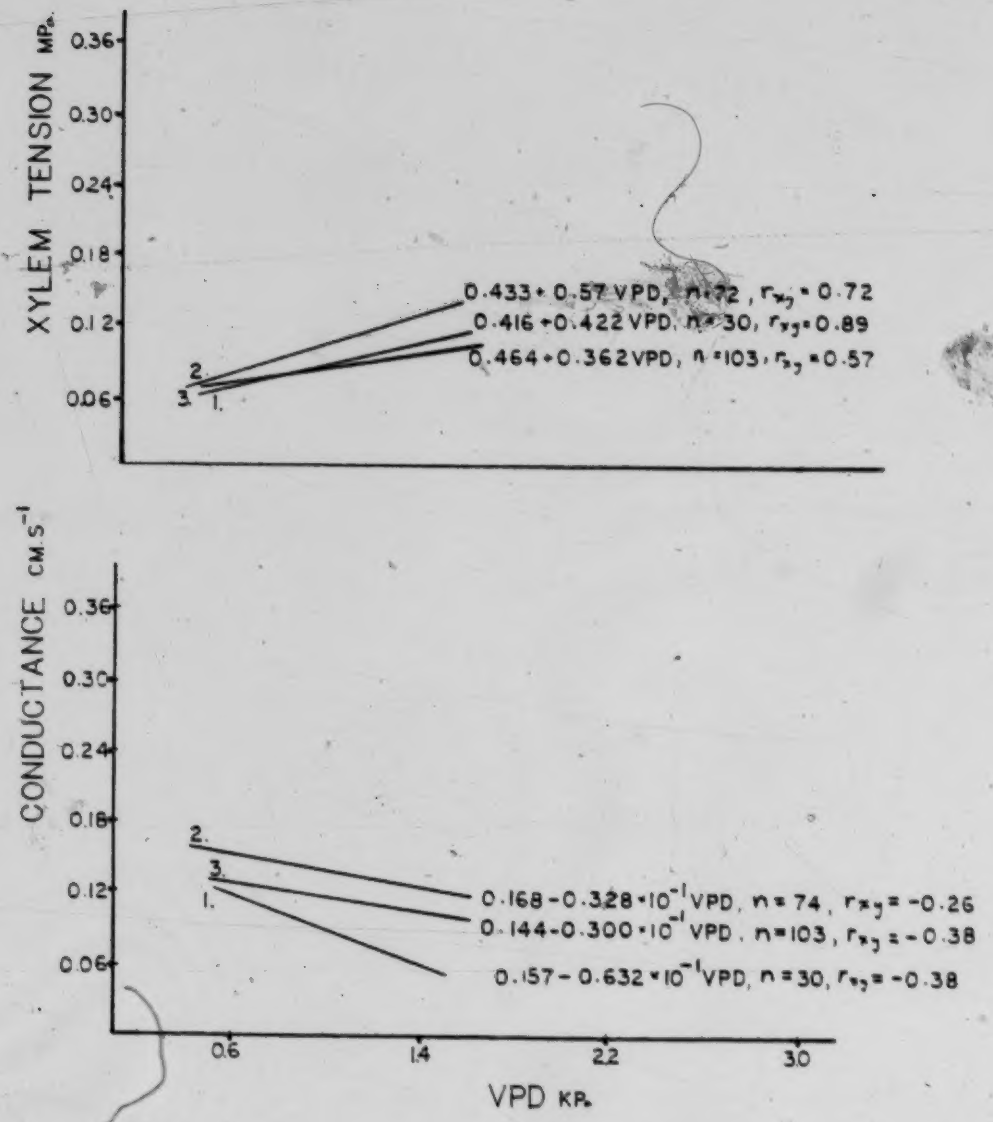


Figure 33 Regression of conductivity and xylem tension against vapor pressure deficit (VPD) for each of 3 clear days. Day 1 was August 2, day 2 was August 9 and day 3 was June 29, 1978.

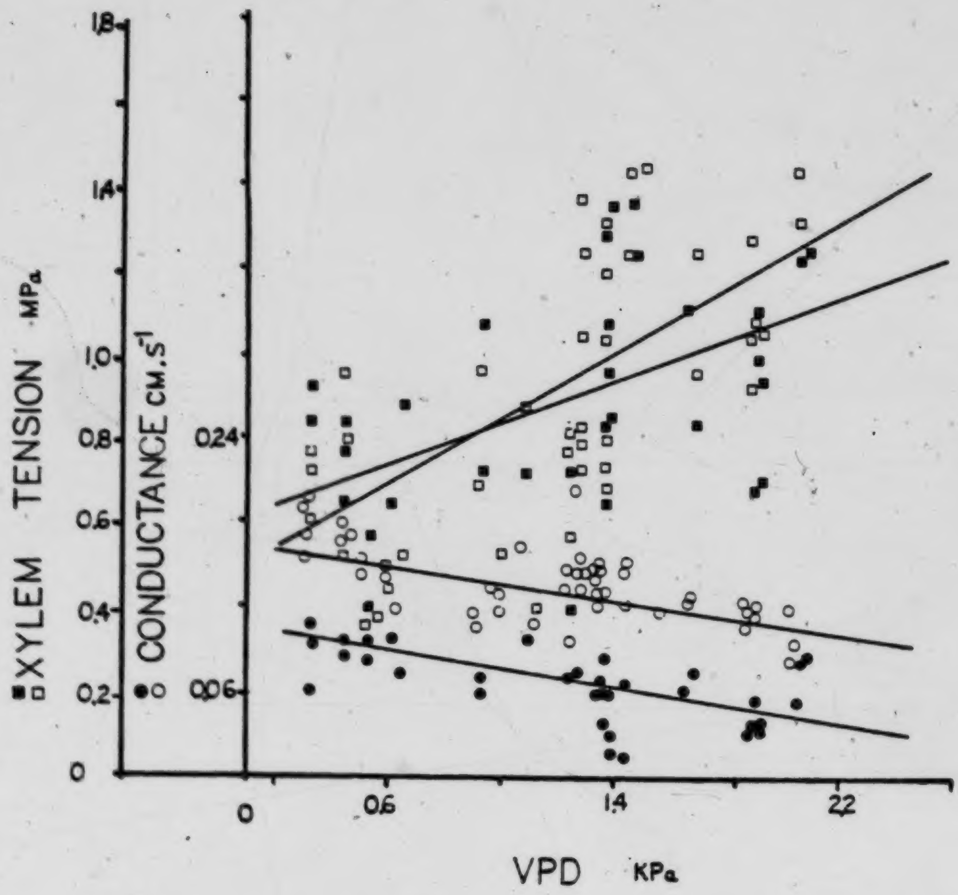


Figure 34 Regression of conductivity and xylem tension against vapor pressure deficit (VPD) for current year (□) and current year plus last year tissue (■) from a Hudsonia-depositional sand site.

In order to more fully understand the important factors in Hudsonia water relations, xylem tension, resistance and water content were matched in time ± 7 min for all data taken in 1977 and 1978. Multiple regressions were performed in order to point out significant correlations between factors (Table 37). Data were divided according to time of day, and xylem tension level as suggested by Figs. 29 and 31. Based upon preliminary analyses, data were split into three time periods per day (0-2400, 0-1200 and 1200-2400 hr) and three ranges of xylem tension (0-3.0, 0-1.4, and 1.4-3.0 MPa). Plant water parameters were regressed against sample height above the ground, length of current and previous years' tissue on the xylem tension sample, total daily radiation, and mean hourly VPD and air temperature. An adequate method of soil water measurement, in numbers suitable for this type of analyses, was not used (temperature flux along Wescor thermocouple soil psychrometers prevented accurate readings). Only factors with a significant correlation were included in the equations. Over the entire range of time of day (0-2400 hr) and xylem tension (0-3.0 MPa), resistance and xylem tension were positively correlated with the amount of previous years' growth and, were negatively correlated with the amount of current year tissue, and were variably correlated to temperature, VPD and radiation. They were variably correlated to each other depending upon the time of day or the level of xylem tension. Resistance was negatively correlated with xylem tension between 1200 and 2400 hr and between 0.0 and 1.4 MPa xylem tension. Resistance was positively correlated with xylem tension between 0-1200 hr and between

Table 37. Summary of multiple regressions for Hudsonia water parameters at the Blowout, 1977 and 1978. Xylem tension (XYL, Mpa units) and resistance (RL, $s.cm^{-1}$ units) were taken on different pieces of tissue, matched in date, time ± 7 min, site and tissue type. Water content (H_2O, % units) was determined from resistance samples, and length (cm) of previous years' tissue (PY , standing dead plus last year tissue), current year tissue (VEG), and sample height above the ground (HT) were determined from xylem tension samples. Radiation (LITE, $MJ.m^{-2}$) was daily total, and air temperature (TEMP, °C) and vapor pressure deficit (VPD, KPa) were hourly means.

Range of sample xylem Tension (MPa x 10^1)	Time period	Dependent variable	Regression	n	Multiple r_{xy}
(A.)					
0-30	0-1200	RL	4.010 +0.339PY +0.114XYL +0.131LITE +0.317HT +0.361VPD -0.175TEMP	353	0.470
0-30	1200-2400	RL	10.620 +1.315PY -0.395VEG +0.185VPD -0.245XYL-0.206LITE+0.179TEMP -0.236HT	535	0.496
0-30	0-2400	RL	7.427 +0.768PY +0.390VPD -0.209VEG -0.113TEMP	888	0.442
0-30	0-1200	XYL	1.568 +0.424TEMP+0.401HT -1.220VEG +0.282PY +0.156RL	353	0.623
0-30	1200-2400	XYL	8.924 +0.095VPD -0.349LITE+0.379TEMP -0.223VEG+0.373PY -0.115RL	535	0.554
0-30	0-2400	XYL	5.798 +0.349TEMP+0.292HT -0.175LITE -0.352VEG+0.314PY	888	0.508
0-30	0-1200	H_2O	85.91 +4.016VPD -3.081XYL	187	0.536
0-30	1200-2400	H_2O	199.9 -4.739LITE+2.793TEMP-2.673RL -3.027XYL-3.210VEG+10.629PY -2.934HT	203	0.552
0-30	0-2400	H_2O	139.9 -1.811HT -1.592LITE-1.546XYL +1.221TEMP-1.008RL	391	0.318
(B.)					
0-14	0-2400	RL	8.535 +0.863PY +0.399VPD -0.273XYL -0.244VEG -0.056LITE	790	0.495
14-30	0-2400	RL	-5.736 +0.613XYL +0.364VPD +0.458PY	98	0.449
0-14	0-2400	XYL	6.319 +0.310TEMP-0.185LITE-0.213VEG +0.260PY -0.090RL+0.072VPD -0.088HT	790	0.653
14-30	0-2400	XYL	15.130 +0.782HT -0.363PY -0.209VPD +0.392LITE+0.124RL-0.261TEMP	98	0.862
0-14	0-2400	H_2O	136.1 -1.968RL +1.394VPD -0.969LITE	331	0.230
14-30	0-2400	H_2O	130.0 +2.23XLY -12.402LITE+8.909TEMP+10.670PY -2.643VPD	59	0.826

1.4 and 3.0 MPa xylem tension. Water content was also positively correlated with VPD and negatively correlated with the amount of current year tissue over the entire range of time of day and xylem tension. In addition, it was negatively correlated to resistance, xylem tension, plant height and radiation. Between 0-1200 hr water content was positively correlated to VPD and negatively correlated to xylem tension. In most cases, VPD and plant tissue characteristics other than xylem tension or leaf resistance, had the largest correlation and influence on the dependent variables, xylem tension, resistance and water content.

Net assimilation temperature optima occurred between 18 and 22°C at 6.5 mg $CO_2 .g^{-1}. hr^{-1}$. The light response for Hudsonia twigs was not saturated at 2000 $uE.m.^{-2}.sec^{-1}$ (Fig. 35). Maximum net assimilation was 9.0 mg $CO_2.g^{-1}.hr^{-1}$.

DISCUSSION

The use of the 'Scholander pressure chamber' to measure leaf water potential has been reviewed by Ritchie and Hinckley (1975). These authors and Bliss and Mayo (1980) point out that a calibration check is required before measurement of xylem tension can be assumed to equal leaf water potential, as determined by the psychometric technique. As with Pinus banksiana from the same study area (Bliss and Mayo, 1980), xylem tensions in Hudsonia did not equal psychrometrically determined stem and leaf water potentials. Xylem tension under-estimated actual leaf and stem water potentials over 0.6

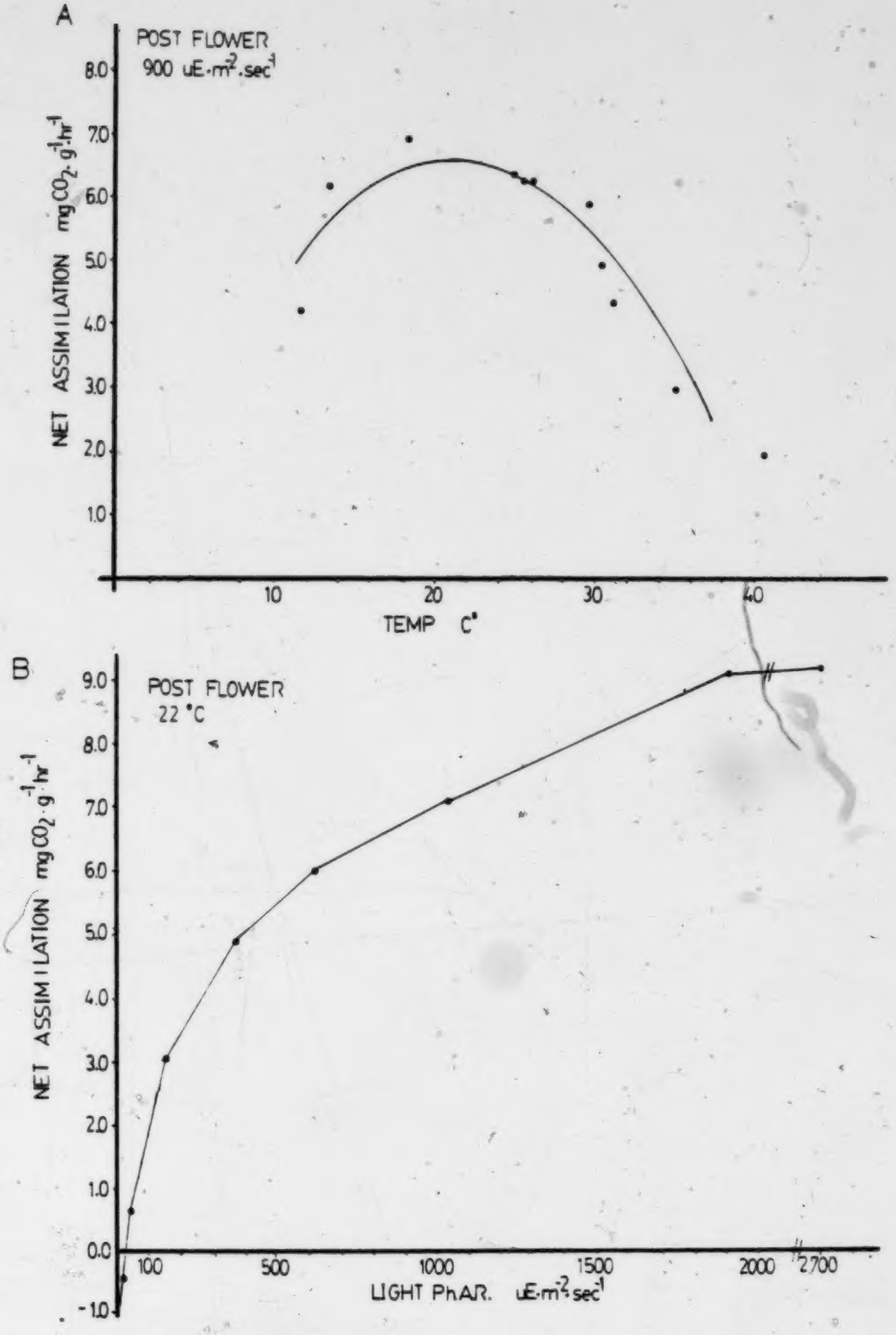


Figure 35 Temperature (A) and light response (B) of Hudsonia net assimilation. Each data point is the mean of 3 in B whereas in A, 3 separate plants were used to derive the data points.

MPa (actual water potential (MPa) = -(7.57 + 2.15 multiplied by xylem tension), correlation coefficient = 0.983, n=12). Therefore, xylem tension was used as an indicator of relative plant water stress and not as an absolute measure of stem and leaf water potential.

The seasonal pattern of xylem tension in Hudsonia was similar to that of many temperate woody broadleaf and semi-evergreen shrubs. For example, Wilkinson (1978), noted that dormancy and overwintering in Ledum groenlandicum was associated with high xylem tensions (>6.0 MPa), as found with Hudsonia. Hudsonia quickly lost any dormancy imposed state of relative dehydration after snowmelt (in at least 3 wk), and then, maintained relatively low (0.5 to 1.95 MPa) but variable xylem tensions throughout the growing season. During both field seasons, no other apparent modification in xylem tension related to seasonality on phenologic events was noted. The meteorological and environmental conditions of the recent past and present appeared to account for the variation noted at any time during the field season. Even the development of fall coloration and formation of buds for next year's growth did not induce detectable changes. Given that Hudsonia, as a means of adaptation to cold, overwinters in the dehydrated state, the anticipated changes in xylem tension and other parameters controlling hydration level must have occurred after mid to late August In contrast, Bliss and Mayo (1980) report that P. banksiana growing in the same area, overwinters in an apparently hydrated state, with xylem tensions depending upon levels at freeze-up.

The range of fluctuation in xylem tension during the growing season was similar to those reported for temperate zone-mesic-woody plants (Ritchie and Hinckley, 1975). They were much lower than values reported for plants adapted to xeric desert areas, such as Salvia, Atriplex and some Juniperus (3.0-6.0 MPa, Scholander et al., 1965). The diurnal course of xylem tension fluctuation in Hudsonia was very similar to that reported for many woody plants under non-limiting soil temperature and moisture conditions (>15.0°C and >0.03 MPa soil water potential-Elfving et al., 1972). A rise from low predawn tensions followed the daily course of radiation and/or VPD until about 1000 hr at which time a plateau xylem tension was reached. Xylem tension then declined from mid-afternoon to predawn values as radiation and/or VPD declined. This pattern was typical for Hudsonia (Figs. 26 and 29) throughout most of both field seasons. However, under conditions of limited precipitation and reasonable levels of radiation and VPD, mid-day mean xylem tension rose, the amplitude of diurnal change increased, and predawn values were not attained during a subsequent dark period (Figs. 26 and 29). A maximum plateau of 1.3 to 1.6 MPa in Hudsonia was similar to a range of values quoted by Lopushinsky (1969) for a variety of temperate zone species (1.5 to 2.5 MPa). This pattern of xylem tension change has been interpreted to indicate soil moisture induced stress (Ritchie and Hinckley, 1975). Failure to rehydrate at night has been attributed to root shrinkage away from the soil and subsequent increase in resistance to water uptake (Taerum, 1973). Although soil water potentials were not determined, values reported for sand from Richardson Fire Tower (MaClean, in Bliss and Mayo, 1980) and for desert sands indicate that at soil water contents of 3 to 5%, soil water potential is below 0.03 MPa. As contents of 3 to 5% were common (0-30 cm profile) it was likely that Hudsonia experienced frequent soil moisture drought as evidenced by xylem tension. However, the high frequency of rain fall combined with the low resistance to infiltration in these sands would check the development of severe soil moisture drought. Only in the 0 to 10 cm profile were extremely dry (< 1.5%) soils found. However, Hudsonia roots were largely outside of this zone. The high frequency of mid-day cloud build-up would also have prevented the development of severe plant water stress. Therefore, it seems unlikely that Hudsonia experienced severe drought and plant water stress during the 1977 or 1978 field season. A higher than normal number of precipitation events occurred, and temperature and moisture conditions were either slightly higher and wetter (1977) or slightly lower and slightly drier in 1978.

Burial experiments indicate that burial decreased the dawn, mid-day and dusk xylem tensions of Hudsonia (Table 36). Sand burial elevated soil temperatures in the vicinity of current year tissue. However, no detrimental influence on plant performance was noted, possibly due to an air space between sand grains and leaf tissue caused by the heavy pubescence. Clearly, a higher evaporative demand and reduced boundary layer resistance on current year tissue or previous years' tissue above ground in the control would result in greater amounts of water loss than in the burial experiments.

The presence of large differences in xylem tension over short distances in Hudsonia are of interest. Several authors have noted spatial differences in xylem tension. For example, Hinckley and Scott (1971) found differences associated with crown position in Douglas Fir and attributed these differences to large differences in environmental conditions. Differences between shade and sun sides of a plant (Kaufmann, 1969) and between needle age class (Sucoff, 1972), have also been noted. In Hudsonia, differences as great as 0.6 MPa were found on current year tissue, within a few cm of tissue length from each other. These differences were also found in depositional-sand sites where self-shading or variability in the microenvironment was limited. Theoretical considerations of hydrostatic pressure and frictional resistance in the xylem only account for a 0.01 MPa drop in xylem tension per meter of height above the ground. This, then, cannot account for the observed differences in Hudsonia. Factors which affect the water balance (loss-supply) must be involved. The involvement of micrometeorological factors, as noted previously, is unknown. However, due to the open nature of Hudsonia plants and communities, it may be that the amount of variation in these factors over short distances at heights 5 cm above the ground, for example, may not be significant. The variability of resistance to water loss from stem and leaf tissue as a result of anatomical, morphological or physiology variability is more likely to be involved. Also, variable resistances to water flow within the stem and between the stem and petiole may also account for these observed differences. In any case, these factors could account for variable plant water status within a plant as a method of drought tolerance at high water potentials. Under drought stress conditions, predetermined parts would suffer a more severe stress as other parts preferentially experienced less stress. Death and abscission of plant parts would result and could in part explain the loss of plant material observed in allocation studies. Catsky (1962) observed perferential movement of water toward younger leaves in Brassica and variable resistance to water flow within stems has been noted (Helkivist et al., 1974).

A related topic is the importance and meaning of differences between initial and endpoint determinations of xylem tension. Ritchie and Hinckley (1975) refer to this as an error associated with certain plant species, variable and lengthy amounts of tissue in and outside of the chamber, inappropriate rates of pressure increase, and passage of air bubbling xylem contents. In Hudsonia, the difference was found to vary on similar tissue and site types depending upon xylem tension, between tissue types, and was more variable as xylem tension was more variable. The variability in xylem tension between tissue types, the influence of height above the ground on xylem tension and increased difference between initial and endpoint xylem tensions, and, variability about a mean with increasing xylem tensions, support the involvement of daily cavitation in the aforementioned abscission of plant parts.

The interpretation of resistance values as an absolute measure of leaf and stem resistance is questionable. Although calibration procedures were precise, the influence of tissue area on final resistances was large. For example, in a sample containing current year and last year tissue, the total area of these tissues was used in the calculations, resulting in a higher resistance. If just current year tissue had been used, resistances would have been lower. The relative contribution of these tissue types to the loss of water was not determined, as the only last year without current year tissue available was dead tissue. Xylem tension and resistance of this dead tissue was variable and often high (>60 sec.cm^{-1}). The noted difference in resistance between current year and current year plus last year tissue (Table 33 and Fig. 34) may be, at least in part, due to the inclusion of last year tissue area into the calculation of resistance.

The high frequency of observed mid-day cloud build-up and precipitation events obscured the attempt to determine Hudsonia's adaptation to drought. It was unclear whether or not stomatal closure was in response to internal water deficit or was coupled directly to VPD. Due to the complexity and variability of microclimatological influences, it remains for controlled environment experiments to determine cause-effect in this regard. However, the analyses (Table 37 and Figs. 32, 33 and 34) indicate that several plant and meteorological variables were involved in the determination of xylem tension and resistance. Strong correlations between the variables and xylem tension or resistance were understood to imply cause-effect only if reasonable explanations were apparent.

In this regard, the elevated mid-day xylem tensions of Hudsonia with a lot of standing dead material (lichen and deflational sites-Tables 33 and 34) were associated with significant plant height (positively correlated to xylem tension). Although height ranged from 0 to 10 cm, evaporative loss, or internal resistances to water flow may have been significant. Also, in the lichen sites the carpet intercepts up to 1.8 $\mathrm{mm.hr^{-1}}$ of precipitation (Lindsay in Bliss and Mayo, 1980). Therefore, under conditions of reduced precipitation, the soil water status became more droughty than the open sands and contributed to a greater level of plant stress. The lichen-site also had higher daily maximum temperature than open sand sites (positively correlated to xylem tension). The noted difference between tissue types within the same site type (Table 34 and Fig. 26) may be explained by the positive correlation of xylem tension with the amount of previous years' tissue.

The positive linear relation between VPD and xylem tension determined over four clear days (Fig. 32), was misleading due to a lack of time of day information in the plot. The bell-shaped relationship between xylem tension and time of day implies that two separate trends (a + and - correlation) exist in Fig. 32. The multiple regression equations (Table 37) support this conclusion as VPD and xylem tension were negatively and positively correlated with VPD between 1.4 to 3.0 and 0 to 1.4 MPa, respectively. No sharp breakpoint or strong curvilinear relation between conductance and VPD were noted (Fig. 32, 33 and 34). This suggests that small reductions in conductance and a combination of micrometeorological parameters reducing evaporative loss were responsible for reduced xylem tensions.

The net assimilation studies for controlled environment grown Hudsonia indicate a lack of high temperature optima. Various species adapted to growth under desert conditions have been noted to have high temperature optima (Bjorkman et al., 1980). However, it is likely that the growth conditions may have preconditioned Hudsonia to these optima and that under field conditions a higher optima could develop. The requirement of high light for saturation of net assimilation most likely relates to the high degree of light reflectance by the pubescence surrounding each leaf.

CONCLUSIONS

Hudsonia tomentosa was found throughout the study area on stabilized and unstabilized aeolian landforms. This thesis has determined that it is *the* major pioneer species after disturbance and colonizes disturbed sites such as roadsides, burn sites, blowouts and dunes. It was often found to be the only vascular plant inhabiting large open sand areas such as the western edge of the Maybelle River Dune System. Observations suggest the following sequence of events and vegetation change for revegetation of open sand on the western edge of the Maybelle River Dune System:

1. the establishment of a *Hudsonia*-sand community either by seeding into an existing *Polytrichum piliferum* sand zone or invasion into open sand,
2. *Hudsonia* dune building resulting in protection of older *Hudsonia* stands,
3. lichenization and *Pinus* seed invasion into older protected *Hudsonia* stands,
4. progress towards lichen and tree canopy closure.

If lichenization and *Pinus* seed invasion are limited, large open semi-stabilized bowls of *P. piliferum* occur. It is likely that a moderate amount of sand deposition is required for *Pinus* invasion. Disturbance results in small blowouts and secondary *Hudsonia* dune building if a supply of sand is available. Seeding-in of *Pinus* appears to be highly variable and is mostly restricted from the open *Hudsonia*-sand communities. Due to secondary disturbances, islands of *Pinus* become isolated and older trees are found in Hudsonia-sand communities. A decline in Hudsonia dominance coincides with lichenization. Hudsonia is of no or decreasing importance in more mesic or less disturbed Pinus-lichen woodlands, and in wetland sites where higher species' diversity occurs.

As mentioned previously, spatial arrangements of plant assemblages in dune environments do not necessarily represent temporal or successional stages. However, Hudsonia's prominance as a pioneer species on open sands raises the question of its role in modifying its environment. Clearly, Hudsonia performs an important role in the initiation of lichenization and is involved in dune building, thereby, affecting wind patterns and neighbouring microclimates. It seems unlikely that any chemical alteration of the sand by Hudsonia results in a favorable condition for Pinus growth. Given the simplicity of the vegetation pattern, it may be unnecessary to search out other roles for Hudsonia in determining vegetation patterns.

Carroll and Bliss (1980) noted a decline in Hudsonia presence in several Alberta and Saskatchewan sites relative to the study area. Carroll (personal comm.) indicated that Hudsonia was absent from large areas of fire disturbed Pinus-lichen woodlands. Morse (1979), suggested that Hudsonia had a much wider distribution in the past, and that the absence of long distance dispersal limited its current distribution. Continued dispersal in open sands ensures the prominence of Hudsonia in dune and blowout sites. However, in closed Pinus-lichen woodlands wind dispersal would be limited to short distances. Given a low frequency of disturbance, mesic site conditions, and a lack of local open sand areas containing Hudsonia, it seems unlikely that Hudsonia can persist. In this regard, it is worthy of note, that the study area represents a more xeric form of the Pinus-lichen woodlands described by Carroll and Bliss (1980), and that, the ridge top blowouts and the large open sand dune systems along the southern shore of Lake Athabasca and in the study area may ensure local Hudsonia prominence.

Before discussing major issues concerning Hudsonia autecology, the major findings and observations of the thesis will be summarized.

Physical site characteristics under which Hudsonia persists were determined at two sites, the Blowout and the western edge of the Maybelle River Dune system. The regional climate is cold temperate with 1000-1500 degree days (5°C base), mean air temperature in the warmest month of $>10°C$, less than 4 months with mean temperature $>10°C$, 307 mm total annual precipitation and moderate to low wind speed (1.5 to 2.0 $m.sec^{-1}$ from May to August).

A consideration of regional meteorological data, after Walter and Leith (1960), indicates that no significant seasonal drought period can be defined for the region due to sufficient rainfall and low mean temperatures in summer.

The soils in which Hudsonia predominates are nutrient poor Orthic Regosols. They are characterized by very high saturation conductivities and limited water storage capacity (Bliss and Mayo, 1980).

When interpreting Hudsonia's performance in various sites within the study area the following site characteristics are most important:

1. All sites receive a high frequency of low intensity precipitation with only occasional cloud bursts. In 1978, 62 of 88 d of observation had detectable precipitation.
2. Soil water contents under lichen-mats are often more moist than in open sand sites. However, more severe drought conditions develop under the lichen mats during extended periods of only low intensity precipitation due to lichen interception (1.8 $mm.hr^{-1}$).
3. Most sand sites experience a varied pattern of wind caused sand deposition and deflation with the mean net deposition and deflation during the summer months of 1977-1979 ranging from 3.5 to 33 $mm.yr^{-1}$ and 0 to 17 $mm.yr^{-1}$, respectively. Maximum net deposition and deflation in Hudsonia occupied sites were 47 $mm.yr^{-1}$ and 17 $mm.yr^{-1}$, respectively.
4. The amount of sand movement that occurred between growing seasons was similar in magnitude to that which occurred within a growing season.
5. Pinus-lichen communities at the western edge of the Maybelle River Dune systems had greater daily maximum and minimum air temperatures and lower average wind speed than the Hudsonia-sand community.
6. At the Blowout site, the maximum daily air temperature was significantly greater (1.0°C) and the minimum daily air temperature and mean monthly wind speed significantly less (1.2°C and 1.3 $km.hr^{-1}$) in the Hudsonia-lichen versus the Hudsonia-sand communities.

Under the above stated site conditions the following phenologic sequence was determined:

1. Hudsonia overwinters in a dehydrated state ($>$6.0 MPa), begins to green-up and attains xylem tensions ($<$2.0 MPa) suitable for metabolic activity soon after snowmelt (ca. early April). The period for bud greening-up can be extensive (April to late May).
2. Large numbers of flowers born on short reproductive shorts develop and flower (early June) before the major period of short extension (mid-June to mid-July). The sequence of flowering within a plant was related to tissue temperature in that south-facing or parts of a plant closest to the ground flower earliest.

3. Early cessation of short extension growth occurs in late July and early August. Bud formation and fall color development coincide with early growth cessation at air temperatures (mean daily air temperatures in August for 1977/78 at the Blowout was 14.5°C) and xylem tensions (< 2.0 MPa) suitable for growth.

This study shows that the level of Hudsonia net annual production and biomass, based on a 1 m^2 analysis, are similar to that found in tundra dwarf shrub and open desert shrub communities (Leith, 1973). Net annual production ranged from 14 to 200 $g.m^{-2}$ and 1 to 140 $g.m^{-2}$ at the Blowout and Dune sites, respectively. The ratio of net annual production to previous years' growth varied considerably with site type, ranging from 0.2 to 50 along the Dune transect and 0.4 to 2.0 within the Blowout communities. The larger ratios were associated with Hudsonia-sand communities experiencing sand deposition and a decline was associated with lichenization.

Analysis of individual twigs (defined as plants p.70) were used to derive correlations between site characters and plant variables. Sand burial and lichen removal experiments were carried out to confirm these correlative determinations.

Both lichen removal and sand burial have significant effects on Hudsonia performance. Lichen removal caused increased allocation to vegetative growth (14 to 60% of net annual production) at the expense of reproductive growth, increased vegetative shoot growth per amount of previous years' growth (0.12 to 0.44), and, increased mean length of vegetative growth (0.14 to 0.34 cm). Moderate levels of sand burial (4.3 cm) stimulated Hudsonia shoot growth by increasing mean length of vegetative growth (from 0.5 to 1.2 cm), and both vegetative (1.4 to

6.3) and net annual production per amount of previous years' growth (2.3 to 7.3). Sand burial also increased allocation to vegetative growth. Both of these experiments support the correlations determined from measures of plant and site variables. For example, % allocation to vegetative growth was negatively correlated with the amount of standing dead and the amount of last year tissue. A directional trend towards reproductive growth versus vegetative in plants with increasing amounts of standing dead was noted at the Maybelle River Dune System mid-dune transect.

Other important findings relating to Hudsonia carbon allocation are:

1. Loss of plant parts between growing seasons indicate that 25-35% of current year tissue was lost between 1977-78 and 1978-79, respectively.
2. Allocation to reproduction was highly variable and varied according to site characteristics and years. For example, the mean allocation to reproduction was 50% in 1978.

Hudsonia plant water relations, as tested during 1977 and 1978 field seasons, were found to be similar to temperate zone woody shrubs. The seasonal pattern of water status, winter desication to >6.0 MPa and rehydration after snowmelt to 0.5 to 1.95 MPa xylem tensions, is more similar to many temperate woody broadleaf and semi-evergreen shrubs than to plants adapted to xeric desert conditions (3.0 to 6.0 MPa during growing season - Scholander et al., 1965). The diurnal course of Hudsonia xylem tension under non-limiting soil moisture conditions and the mid-day maximum plateau (1.3 to 1.6

MPs) are similar to that found for a variety of temperate zone plants (1.5 to 2.5 MPa, Elfving et al., 1972 and Lopushinsky, 1969). Also, as noted in several plant species, a period of reduced precipitation result in an increase in pre-dawn xylem tensions (Ritchie and Hinchley, 1975).

Correlations between measures of plant status and site and plant variables showed that xylem tension and leaf resistance to water loss were positively correlated with amount of previous years' growth, negatively correlated to amount of current year growth, and variably correlated to temperature, vapor pressure deficit, radiation, height above the ground and each other depending upon the time of day. Site differences were found and were mostly explained through correlations between site and plant variables with either xylem tension or leaf resistance. For example, the greater mid-day xylem tensions in the Hudsonia-lichen (1.75 MPa) versus the Hudsonia-sand with (1.40 MPa) and without (1.09 MPa) standing dead were explained by the positive correlation between xylem tension and the amount of standing dead height above the ground and air temperature.

Sand burial experiments confirmed these correlations, and showed that sand burial lowered dawn and mid-day xylem tensions by 0.17 MPa and 0.37 MPa, respectively.

Although xylem tensions followed the diurnal course of vapor pressure definit (VPD) and varied as the daily amplitude of VPD varied, it remains unclear whether or not mid-day stomatal closure is in response to water deficits or is coupled directly to VPD. Due to a high frequency of mid-day cloud build-up and precipitation events, the development of excessive plant water stress in Hudsonia is prevented by small decreases in stem and leaf conductance, either in response to VPD or xylem tension. Only after extensive periods of reduced precipitation would severe enough drought conditions develop to test the limits of Hudsonia's survival.

The extent of variability in water status of similar tissue types over short distances (1 cm) within a plant (0.6 MPa) and the differences between initial and endpoint determinations of xylem tension indicate a preferential maintenance of plant water status within a Hudsonia plant. Thus, variable stem and leaf resistance to water loss and/or variable stem resistances to water flow may account for the observed abscission of plant parts and ensure survival of the individual under more severe drought conditions.

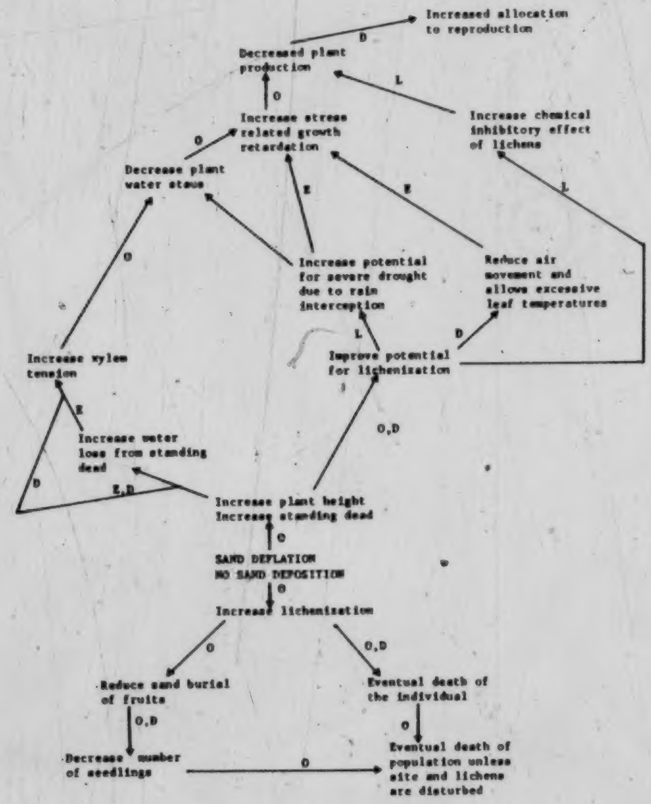
In terms of soil plant interactions, this study has determined that Hudsonia possesses a free-living nitrogen-fixing microbial association. The extent and nature of noted mycorrhizal associations was not determined. Hudsonia was found to be the only vascular plant for which nitrogen fixation was detected. Nitrogen fixation rates, as measured by acetylene reduction, were low (maximum rate of 1 nmole C_2H_4.g soil^{-1}hr.$^{-1}$) but were probably significant in these nutrient poor sites. Fixation rates showed seasonal trends with maximum rates occurring at ca. 30% soil water content, 28-33°C and in the absence of a nitrogen source other than N_2 gas. Blue green algae (Oscillatoria, Lyngbya, Nostacaceae-type and Microcystis) appear to be responsible for the nitrogen fixation detected in the rhizosphere and buried phyllosphere of Hudsonia. This free-living nitrogen-fixing blue green algal association is unique to Hudsonia and warrants further investigation.

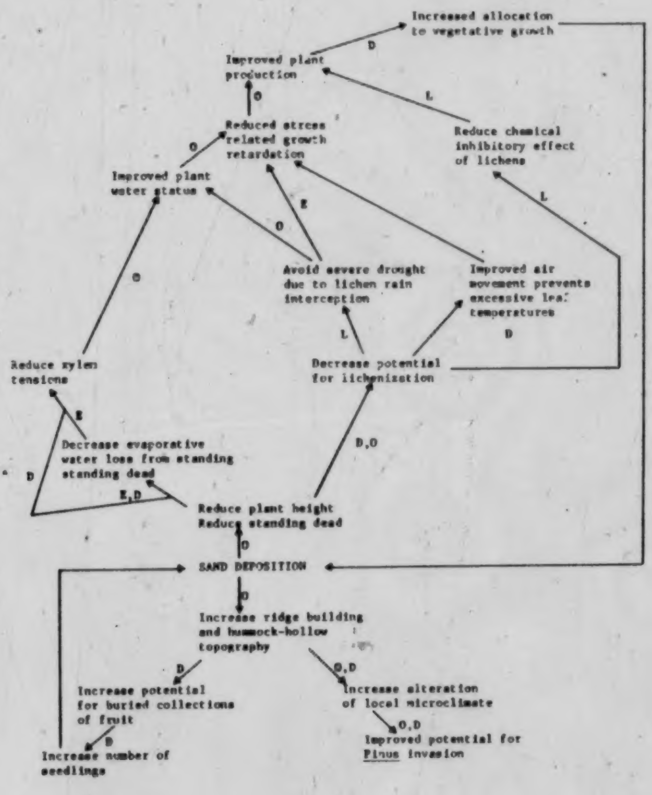
The nutrient requirements of Hudsonia were not determined, however, several observations relate to Hudsonia's ability to grow on these nutrient poor sands. As summarized in Chapin (1980) and Grime (1979), a list of attributes associated with plants from nutrient poor as compared to more fertile sites includes: low levels of inorganic nitrogen, reduced nutrient leaching from tissue, greater than 50% nutrient retranslocation to other plant parts before abscission, increased leaf longevity, slower growth rates, large root:shoot ratios, low root turnover, low root absorption capacity and increased rhizosphere interactions. Clearly Hudsonia possess certain of these attributes, such as mycorrhizal and N_2 fixing rhizospheric interactions. Given the potential for large amounts of Hudsonia leachate resulting from sand abrasion, the ability of mycorrhizae and other soil microbes to absorb and contain nutrients in the rhizosphere and buried phyllosphere system may also be important. In addition, the water absorbing and retention abilities of algal and fungal populations in the rhizosphere and buried phyllosphere may play a significant role in improving overall plant water status. This occurs by prevention of rapid infiltration of precipitation into the sand and by reducing evaporative losses. Internal cycling of nutrients is likely to occur, as noted in several other semi-evergreen broadleaf shrubs grown in nutrient poor sites (Chapin, 1980 and Grime, 1979) Studies on the root turnover, absorption capabilities and seasonal nutrient and carbohydrate levels may also provide explanations for Hudsonna's prominance in those sites. However, Hudsonia root:shoot ratios were low (0.26 to 0.34 as compared to 0.60 to 0.70 for dwarf ericaceous shrubs - Larcher 1973).

In the author's view, given normal climatic conditions, sand movement is the most determining factor in these communities and plays a major role in determining species distribution and plant vigor. Hudsonia growth and water status has been shown to be improved by moderate amounts of sand deposition, and several plant parameters are correlated with the level of sand deposition. These include: net annual production (+), allocation to vegetative growth (+), allocation to reproductive growth (-), mean length of vegetative growth (+), total length of shoot growth per plant (+), and the amounts of vegetative (+), reproductive (-) and net annual production (+) per amount of previous years' growth. Also, growth characteristics and plant water relations parameters are correlated with plant and site variables which relate to the level of sand deposition, for example, xylem tension is positively correlated with plant height and amount of standing dead. Most sites have a varied pattern of both deflation and deposition. Variations in plant growth and allocation indicate a flexibility in Hudsonia's growth habit which allows Hudsonia to respond to this varied pattern of sand deposition and deflation. These variations and the eventual fate of Hudsonia after lichenization can be better understood by noting the correlations between these site and plant variables. A word model depicts these interactions, based on the effects of sand deposition or deflation (Fig. 36). For example, in the lichen community or sand community with standing dead, reduced annual production is most likely the result of decreased plant water status and stress induced inhibition of the growth. Sand burial reduces evaporative water loss from supporting tissue. If prolonged periods without high intensity precipitation occur, increased soil moisture stress would occur under the lichen carpet, whereas low intensity precipitation would infiltrate open sands and aid improvement of plant water status. The correlations between burial and carbon allocation, between burial and water status implies that allocation to reproductive growth is favored in sites without sand deposition. Varied deposition and deflation, if moderate, would maintain Hudsonia vegetative growth in open sand sites. However, an overall trend towards reproductive growth and plant decline in sites without significant sand deposition, such as lichen sites, is predicted, possibly due to the increased probability of severe drought and the influence of plant water status on allocation. The role of chemical inhibitors from lichens is suggested from work by Brown (1967) and Brown and Mikola (1974).

It may be, as indicated in Bliss and Mayo (1980), that a one in 25 or 50 year drought may indeed determine the limits of species survival in the region. In terms of other plant species, it may be an attribute related to plant water status and its control, rather than flexibility

Figure 36. The fate of Hudsonia in response to sand deposition or deflation. The events above the indicator SAND DEPOSITION or SAND DEFLATION refer the individual plant whereas those below refer to the community. The arrows indicate the direction of change and the letters refer the source of information (L -literature, D -data in thesis, O -observed or obvious and E - expected).


Increased allocation to reproduction
D
Decreased plant production
L
O
Increase stress related growth retardation
Increase chemical inhibitory effect of lichens
O
Decrease plant water staus
E
E
L
Increase potential for severe drought due to rain interception
Reduce air movement and allows excessive leaf temperatures
O
L
D
Improve potential for lichenization
Increase xylem tension
E
O,D
Increase water loss from standing dead
D
E,D
Increase plant height
Increase standing dead
O
SAND DEFLATION
NO SAND DEPOSITION
O
Increase lichenization
O
O,D
Reduce sand burial of fruits
Eventual death of the individual
O,D
O
Decrease number of seedlings
O
Eventual death of population unless site and lichens are disturbed


Increased allocation to vegetative growth
D
Improved plant production
L
O
Reduced stress related growth retardation
Reduce chemical inhibitory effect of lichens
O
Improved plant water status
E
L
O
Avoid severe drought due to lichen rain interception
Improved air movement prevents excessive leaf temperatures
O
L
D
Decrease potential for lichenization
Reduce xylem tensions
E
D,O
Decrease evaporative water loss from standing standing dead
D
E,D
Reduce plant height
Reduce standing dead
D
SAND DEPOSITION
D
Increase ridge building and hummock-hollow topography
D
O,D
Increase potential for buried collections of fruit
Increase alteration of local microclimate
D
O,D
Increase number of seedlings
Improved potential for Pinus invasion

of response to sand movement which determines Hudsonia's dominance as a pioneer species on these open sands.

In conclusion, the potential for use of Hudsonia in the revegetation of Alberta's Oil Sands remains unclear. However, Hudsonia tomentosa exhibits several adaptations for growth and survival on the xeric nutrient poor sands. It represents the only native plant species, involved in revegetation, able to colonize and persist in the open sand areas. Revegetation trials with agronomic grasses (Selner and Thompson, 1977), and with trees and shrubs (Vartnou, 1976) have proved mostly unsuccessful due to high fertilizer and irrigation maintenance and pest problems. Given a long-term objective for the revegetation of these areas, management strategies should include a serious consideration of Hudsonia.

REFERENCES

Addison, P.A. 1977. Autecology of Luzula confusa, Ph.D. Thesis. Botany Department, University of Alberta. 160 pp.

Allen, E.M., O.N. Allen and C.J. Klebesadel. 1964. An insight into symbiotic nitrogen-fixing plant associations in Alaska. Proc. Alaskan Sci. Conf. 14th Anchorage Alaska 54.

Allen, M.M. and R.Y. Stanier. 1968. Selective isolation of blue green algae from water and soil. J. Gen. Microbiol. 51: 203-209.

Arnon, I. 1975. Physiological principles of dryland crop production. In, 'Physiological Aspects of Dryland Farming.' U.S. Gupta (Ed.), New Delhi, Bombay, and Calcutta, Oxford. pp.3-145.

Bayrock, L.A. 1969, 1970. Helicopter survey field notes for N.T.S. map sheets 74L and 74E (Bitumount, Fort Chipewyan Alberta). Research Council of Alberta files. 124 pp.

Becking, J.H. 1977. Dinitrogen - fixing associations in higher plants other than legumes. In, 'A Treatise on Dinitrogen Fixation, Section III: Biology.' R.W.F. Hardy and W.S. Silver (Eds.). John Wiley and Sons, Toronto. pp.185-277.

Begg, J.E. and N.C. Turner. 1970. Water potential gradients in field tobacco. Pl. Physiol. 46: 343-346.

Begg, J.E. and B.W.R. Torssell. 1974. Mechanisms of regulation of plant growth. Bull. R. Soc. N.Z. 12: 277-282.

Begg, J.E. and N.C. Turner. 1976. Crop water deficits. Adv. Agron. 28: 161-217.

Bjorkman, O., M.R. Badger, and P.A. Armond. 1980. Response and adaptation of photosynthesis to high temperatures. In, 'Adaptation of Plants to Water and High Temperature Stress.' p.233-249. N.C. Turner and P.J. Kramer (Eds.). John Wiley & Sons, New York. pp.233-249.

Black, R.A. and L.C. Bliss. 1979. Reproduction ecology of Picea mariana (Mill.) BSP., at tree line near Inuvik, Northwest Territories, Canada. Ecol. Monogr. 50: 331-354.

Bliss, L.C. and J.M. Mayo. 1980. An ecophysiological investigation of the jack pine woodland with reference to revegetation of mined sands. Alberta Oil Sands Environ. Res. Program. Dept. Environ. Edmonton, Alta.

Blum, A. 1975. Effect of the BM gene on epicultlcular wax and the water relations of Sorghum Bicolor I. Israel J. Bot. 24: 50-51.

Bond, R.D. and J.R. Harris. 1964. The influence of the soil microflora on physical properties of the soil. I. Effects associated with filamentous algae and fungi. Aust. J. Soil Res. 2: 111-122.

Booth, W.E. 1941. Algae as pioneers in plant succession and their importance in erosion control. Ecology. 22: 38-46.

Boyer, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Pl. Physiol. 46: 233-235.

Boyer, J.S. 1971. Resistance to water transport in soybean, bean and sunflower. Crop Sci. II: 403-407.

Bristow, J.M. 1974. Nitrogen fixation in the rhizosphere of freshwater angiosperms. Can. J. Bot. 52: 217-223.

Brown, K.W., W.R. Jordan, and J.C. Thomas. 1976. Water stress induced alterations of the stomatal response to decreases in leaf water potential. Physiol. Pl. 37: 1-5.

Brown, R.J. 1967. Influence of naturally occurring compounds on germination and growth of jack pine. Ecology. 48: 542-546.

Brown, R.J. and P. Mikola. 1974. The influence of fruiticose soil lichens upon the mycorrhizae and seedling growth of forest trees. Acta For. Fenn. 141: 1-23.

Brubaker, L.B. 1975. Postglacial forest patterns associated with till and outwash in north central Upper Michigan. Quat. Res. 5:499-527.

Bryson, R.A. and W.M. Wendland. 1967. Tentative climatic patterns for some late-glacial and post-glacial episodes in central North America. Tech. Rept. 34, Nom. 1202 (07), Dept. Meteor., Univ. Wisconsin, Madison, 32 pp.

Bunce, J.A. 1978. Effect of shoot environment on apparent root resistance to water flow in whole soybean and cotton plants. J. Exp. Bot. 29: 595-601.

Burch, G.J., R.C.G. Smith, and W.K. Mason. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. II. Crop evaporation, soil water depletion and root distribution. Aust. J. Pl. Physiol. 5: 169-177.

Caldwell, M.M., 1976. Root extension and water absorption. In, 'Water and Plant Life: Problems and Modern Approaches.' O.L. Lange, L. Kappen, and E.D. Schulze (Eds.), Springer-Verlag, Berlin and Heidelberg. pp.63-85.

Camacho, B.S.E., A.E. Hall, and M.R. Kaufmann. 1974. Efficiency and regulation of water transport in some woody and herbaceous species. Plant Physiol. 54: 169-172.

Cameron, R.E. and W.H. Fuller. 1960. Nitrogen fixation by some soil algae in Arizona soils. Soil Sci. Soc. Am. Proc. 24: 353-356.

The Canadian System of Soil Classification. 1978. Research Branch, Canada Dept. of Agric., Ottawa. 164 pp.

Carroll, S.B. and L.C. Bliss. 1982. Jack pine - lichen woodland on sandy soils in northern Saskatchewan and northeastern Alberta. Can. J. Bot. 60: 2270-2282.

Catsky, J. 1962. Water saturation deficit in the wilting plant. The preference of young leaves and the translocation of water from old into young leaves. Biologia Pl. 4: 306-314.

Cayford, J.H. and D.J. McRae. 1981. The ecological role of fire in jack pine forests. In, 'Fire in Northern Circumpolar Ecosystems.' R.W. Wein (Ed.). John Wiley and Sons, Toronto. 332 pp.

Chapin, F.S. III. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.

Chepil, T. 1958. Soil conditions that influence wind erosion. Tech. Bull. U.S. Dept. Agric. # 1185.

Clayton, J.S., W.A. Chrlick, D.B. Can, J.H. Day, and J.B. Marshall. 1977. Soils of Canada. Volume 1. Can. Dep. Agric., Ottawa, 243 pp.

Constable, G.A., and A.B. Hearn, 1978. Agronomic and physiological response of soybean and Sorghum crops to water deficits. I. Growth, development and yield. Aust. J. Pl. Physiol. 5: 159-167.

Cooper, W.S. 1958. Coastal sand dunes of Oregon and Washington. Mem. Geol. Soc. Amer. 72. pp.1-169.

Crum, H. 1976. Mosses at the Great Lakes Forest. University of Michigan, Ann Arbor. 404 pp.

David, P.P. 1977. Sand dune occurrences of Canada. A theme and resource inventory study of aeolian landforms of Canada. Canada Dept. Indian & North. Aff., Natl. Parks Branch, Contract 74-230. 183 pp.

David, P.P. 1981. Stabilized dune ridges in northern Saskatchewan Canad. J. Earth Sci. 18: 286-310.

Dimond, A.E. 1966. Pressure and flow relations in vascular bundles of the tomato plant. Pl. Physiol. 41: 119-131.

Dobereiner, J., J.M. Day, and P.J. Dart. 1972. Nitrogenase activity in the rhizosphere of sugar cane and some other typical grasses. Plant and Soil. 37: 191-196.

Durrell, L.W. and L.M. Shields. 1961. Characteristics of soil algae relating to crust formation. Trans. Am. Microsc. Soc. 80: 73-79.

Ehleringer, J., O. Bjorkman, and H.A. Mooney, 1976. Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub, Science. N.Y. 192: 376-377.

Elfving, D.C., M.R. Kaufmann, and A.E. Hall. 1972. Interpreting leaf water potential measurements with a model of the soil plant atmosphere continuum. Physiol. Pl. 27: 161-168.

Evenari, M., L. Shanan, and N. Tadmor. 1971. The Negev: The Challenge of a Desert. Cambridge, Massachusetts: Harvard Univ. Press.

Fischer, R.A., and N.C. Turner. 1978. Plant productivity in the arid an semi-arid zones. Ann. Rev. Pl. Physiol. 29: 277-317.

Fletcher, J.E. and W.P. Martin. 1948. Some effects of algae and molds in the rain crust of desert soils. Ecology. 29: 95-100.

Flint, H.L. 1974. Phenology and genecology of woody plants. In, 'Phenology and Seasonality Modeling'. Ecological Studies 8. H. Leith (Ed.). Springer-Verlag, New York. 443 pp.

Fogg, G.E. 1952. The production of extracellular nitrogenous substances by a blue-green algae. Proc. Roy. Soc. Lond. B. 139: 372-373.

Fogg, G.E. and Than-Tun. 1960. Interrelations of photosynthesis and assimilation of elementary nitrogen in a blue-green alga. Proc. Roy. Soc. Lond. B. 153: 111-127.

Fogg, G.E. and W.D.P. Stewart. 1968. In-situ determinations of biological nitrogen fixation in Antarctica. Br. Antarct. Surv. Bull. 15: 39-46.

Fogg, G.E., W.D.P. Stewart, P. Fay, and A.E. Walsby. 1973. The Blue-Green Algae. Acad. Press London. 459 pp.

Fritsch, F.E. and E.J. Salisbury. 1915. Further observations on the heath association on Hinhead Common. New Phytol. 14: 116-138.

Gadgil, M.D. and O.T. Solbrig. 1972. The concept of r- and k-selection: evidence from wild flowers and some theoretical considerations. Amer. Natur. 106: 14-31.

Gardner, W.R. 1973. Internal water status and plant response in relation to the external water regime. In, 'Plant Response to Climatic Factors.' R.O. Statyer (Ed.). Unesco, Paris, pp.221-225.

Gorham, P.R., J.S. McLachlan, U.J. Hammer, and W.K. Kim. 1964. Isolation and culture of toxic strains of Anabaena flosaguae (Lyngb) de Breb. Verb Int. Ver. Theor. Limnol. 15: 796-804.

Green, P.B., R.O. Erickson, and J. Buggy. 1971. Metabolic and physical control of cell elongation rate in vivo studies in Nitella. Pl. Physiol. 47: 423-430.

Gresham, C.A., T.R. Sinclair, and J.E. Wuenscher. 1975. A ventilated diffusion porometer for measurement of stomatal resistance of pine fasciles. Photosynthetics 9: 72-77.

Grime, J.P. 1979. Plant Strategies and Vegetation Process. John Wiley and Sons, New York. 222 pp.

Hale, M.E. 1969. The Lichens. Wm. C. Brown Publishers. Dubuque, Iowa. 226 pp.

Hall, A.E., and M.R. Kaufmann. 1975. Regulation of water transport in the soil-plant atmosphere continuum. In, 'Perspectives of Biophysical Ecology. Ecological Studies, Vol. 12.' D.M. Gates and R.B. Schmerl (Eds.). Springer-Verlag, New York. pp.187-202.

Hall, A.E., E.D. Schulze, and O.L. Lange. 1976. Current perspectives of steady state stomatal responses to environment. In, 'Water and Plant Life, Problems and Modern Approaches.' O.L. Lange, L. Kappen, E.D. Schulze (Eds.), Springer-Verlag, New York. pp.169-188.

Hall, M.T. 1956. Variation in the genus Hudsonia. Proc. Indiana Acad. Sci. 66: 321-322.

Hardy, R.W.F., R.C. Burns, R.R. Hebert, R.D. Holsten, and E.K. Jackson. 1971. Biological nitrogen fixation: a key to world protein. Plant and Soil. Special Vol. pp.561-590.

Hardy, R.W.F. and R.D. Holsten. 1977. Methods for measurement of dinitrogen fixation. In, 'A Treatise on Dinitrogen Fixation, Section IV: Agronomy and Ecology.' R.W.F. Hardy and A.H. Gibson (Eds.) John Wiley and Sons, Toronto, pp.451-486.

Harper, J.L. 1977. 'Population biology of plants.' Academic Press, London. 892 pp.

Harper, J.L. and J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to Senecio vulgaris L. J. Ecol. 58: 681-698.

Hassouna, M.G. and P.F. Wareing. 1964. Possible role of rhizosphere bacteria in the nitrogen nutrition of Ammophila arenaria. Nature. 202: 467-469.

Hellkvist, J., G.P. Richards, and P.G. Jarvis. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. J. Appl. Ecol. II: 637-667.

Henriksson, E. 1971. Algal nitrogen fixation in temperate regions. Plant and Soil. Special Vol. pp.415-419.

Hermesh, R. 1972. A study of the ecology of the Athabasca sand dunes, with emphasis on the phytogenic aspects of dune formation. M.Sc. Thesis. Dept. Plant Ecol., Univ. Saskatchewan, Saskatoon. 158 pp.

Hinckley, J.M., and D.R.M. Scott. 1971. Estimates of water loss and its relation to environmental parameters in Douglas fir saplings. Ecology 52: 520-524.

Hsiao, J.C. 1973. Plant responses to water stress. Ann. Rev. Pl. Physiol. 24: 519-570.

Hsiao, J.C., and E. Acevedo. 1974. Plant responses to water deficits, water use efficiency, and drought resistance. Agric. Meteorol. 14: 59-84.

Hsiao, L.C., E. Acevedo, E. Fereres, and D.W. Henderson. 1976. Stress metabolism (water stress, growth, and osmotic adjustment). Phil. Trans. R. Soc. B. 273: 479-500.

Johnson, D.A. 1978. Environmental effects on turgor pressure response in range grasses. Crop. Sci. 18: 945-948.

Johnson, E.S. and J.S. Rowe. 1977. Fire and vegetation change in the western subarctic. Can. Dept. Indian North. Affairs. Arctic Land Use Res. 75-76-61. Ottawa.

Jones, M.M., and N.C. Turner. 1978. Osmotic adjustment in leaves of sorghum in response to water deficits. Pl. Physiol. 61: 122-126.

Jones, M.M., N.C. Turner, and C.B. Osmond. 1979. Mechanisms of drought resistance. In, Physiology and Biochemistry of Drought Resistance.' L.G. Paleg and D. Aspinall (Eds.), Academic Press, New York, pp.15-37.

Jones, M.M., and H.M. Rawson. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency, and osmotic potential in sorghum. Physiol. Pl. 45: 103-111.

Jurgensen, M.F. and C.B. Davey. 1968. Nitrogen fixing blue-green algae in acid forest and nursery soils. Can. J. Microbiol. 14: 1179-1183.

Kaufmann, M.R. 1969. Relation of slice gap width in oranges and plant water stress. J. Am. Soc. Hort. Sci. 94: 161-163.

Kenyon, C.N., R. Rippeka and R.G. Stanier. 1972. Fatty acid composition and physiological properties of some filamentous blue green algae. Arch. Mikrobiol. 83:216-236.

Kershaw, K.A. and W.R. Rouse. 1976. The impact of fire on forest and tundra ecosystems. Can. Dept. Indian North. Affairs. Publ. No. 8117-000-EE-A1. Ottawa.

Khoja, T. and B.A. Whitton. 1972. Heterotrophic growth of blue-green algae. Arch. Microbiol. 79: 280-282.

Knowles, R. 1977. The significance of asymbiotic dinitrogen fixation by bacteria. In, 'A Treatise on Dinitrogen Fixation, Section IV: Agronomy and Ecology.' R.W.F. Hardy and A.H. Gibson (Eds.). John Wiley and Sons, Toronto. pp.33-84.

Kramer, P.J. 1969. Plant and Soil Water Relationships: A Modern Synthesis. McGraw-Hill, New York. 449 pp.

Kramer, P.J. 1980. Drought, stress, and the origin of adaptations. In, 'Adaptation of Plants to Water and High Temperature Stress.' N.C. Turner and P.J. Kramer (Eds.). John Wiley & Sons, New York. pp.7-20.

Landals, M. 1978. Lake Athabasca sand dunes. A survey of preservation and recreation values of the sand dunes and surrounding area. (Personal comm.)

Lansley, A.G. 1953. The British Islands and Their Vegetation. 2 vols. Cambridge Univ. Press, Cambridge. 930 pp.

Larcher, W. 1975. Physiological Plant Ecology. Springer-Verlag, New York. 252 pp.

Larson, D.W. and K.A. Kershaw. 1976. Studies on lichen dominated systems. XVIII. Morphological control of evaporation in lichens. Can. J. Bot. 54: 2061-2073.

Lee-Stadelmann, O.Y., and E.J. Stadelmann. 1976. In, 'Water and Plant Life: Problems and Modern Approaches.' O.L. Lange, L. Kappen, and E.D. Schulze (Eds.), Springer-Verlag, New York. pp.268-280.

Levitt, J. 1972. 'Responses of Plants to Environmental Stresses.' Academic Press, NY. 697 pp.

Lex, M., W.B. Silvester, and W.D.P. Stewart, 1972. Photorespiration and nitrogenase activity in the blue-green alga, Anabaena cylindrica. Proc. Roy. Soc. Lond. B. 180: 87-102.

Lieth, H. 1973. Primary production: terrestrial ecosystems. Human Ecology 1:303-332.

Longley, R.W. and B. Janz. 1978. The climatology of the Alberta Oil Sands Environmental Research Program study area. Prep. for the Alberta Oil Sands Environmental Research Program by Fisheries and Environment Canada, Atmospheric Environment Services. AOSERP Report 39. 102 pp.

Lopushinsky, W. 1969. Stomatal closure in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 130: 258-263.

Lowe, P. 1977. An approximating polynomial for the computation of saturation vapor pressure. J. Appl. Meteor. 16: 100-103.

Ludlow, M.M. 1975. Effect of water stress in the decline of leaf photosynthesis with age. In, 'Environmental and Biological Control of Photosynthesis.' R. Marcelle (Ed.). Junk, The Hague. pp.123-134.

Mague, T.J. 1977. Ecological aspects of dinitrogen fixation by blue-green algae. In, 'A Treatise on Dinitrogen Fixation, Section IV: Agronomy and Ecology.' R.W.F. Hardy and A.H. Gibson (Eds.). John Wiley and Sons, Toronto. pp.85-140.

Maikawa, E. and K.A. Kershaw. 1976. Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce - lichen woodland in the Abitau Lake Region, N.W.T. Can. J. Bot. 54: 2679-2687.

Mallard, T.M., C.S. Mallard, H.S. Holfeld, and T.A. LaRue. 1977. Inexpensive portable gas chromatograph for the acetylene reduction assay for nitrogenase. Anal. Chem. 49: 1275-1277.

Martin, T.L. 1939. The occurrence of algae in some virgin Utah soils. Soil Sci. Soc. Amer. Proc. 4: 249-250.

Marks, C.G. and T.A. Kozlowski. 1973. Ectomycorrhizae. Acad. Press. N.Y. 444 pp.

May, C.H. and F.L. Milthorpe. 1962. Drought resistance of crop plants. Field Crop Abstracts 15:171-179.

Mayland, H.F. and J.H. McIntosh. 1966. Availability of biologically fixed atmospheric nitrogen -15 to higher plants. Nature, 209: 421-422.

Mayo, J.M. 1974. A thermocouple psychrometer chamber for field and laboratory use. Can. J. Plan. Sc. 54: 597-598.

McIain, K.M. and K.A. Armson. 1975. Growth responses of pine and spruce seedlings to regimes of soil moisture and fertility. Soil. Sci. Soc. Amer. Proc. 39:140-144.

McCree, K.J. 1974. Changes in the stomatal response characteristics of grain sorghum produced by water stress during growth. Crop Sci. 14: 274-278.

Meidner, H., and M. Edwards. 1975. Direct measurements of turgor pressure potentials of guard cells, I. J. Exp. Bot. 26: 319-330.

Millbank, J.W. and K.A. Kershaw. 1970. Nitrogen metabolism in lichens. III. Nitrogen fixation by internal cephalodia in *Lobaria pulmonaria*. New. Phytol. 69: 595-599.

Monthly record of meteorological observations and Canadian normals. (1941-1970). Pub. by Atmospheric Environment, Dept. of Fisheries and Environ. Can.

Morgan, J.M. 1977. Differences in osmoregulation between wheat genotypes. Nature (London) 270: 234-235.

Morgan, J.M. 1980. Osmotic adjustment in the rakelets and leaves of wheat. J. Exp. Bot. 31: 655-665.

Morse, L. 1979. Systematics and ecological biogeography of the genus. *Hudsonia* (Cistaceae), the sand heathers. Ph.D. Thesis. Harvard Univ. 275 pp.

Moss, E.H. 1959. 'Flora of Alberta.' Univ. of Toronto Press, Toronto. 546 pp.

Mosse, B., D.S. Hayman, and D.J. Arnold. 1973. Plant growth responses to vesicular-arbuscular mycorrhiza. New Phytol. 72: 809-815.

Nielson, B. 1978. The potential for wilderness recreation in a sand dune environment. M.Sc. Thesis. Geography Department, University of Alberta. 138 pp.

Ogden, J. 1974. The reproductive strategy of higher plants. II. The reproductive strategy of *Lussilago farfara L.* J. Ecol. 62: 291-324.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. 119: 125-170.

Orsham, G. 1963. Seasonal dimorphism of desert and mediterranean chamaephytes and its significance as a factor in their water economy. In, 'The Water Relations of Plants.' A.J. Rutter and F.H. Whitehead (Eds.). Blackwell Scientific Publications. London. pp. 206-222.

Parker, J. 1968. Drought-resistance mechanisms. In, 'Water Deficits and Plant Growth.' Vol. 1. L.L. Kozlowski (Ed.). Academic Press, New York. pp.195-234.

Paul, E.A., R.J.K. Myers, and W.A. Rice. 1971. Nitrogen fixation in grassland and associated cultivated ecosystems. In, 'Biological Nitrogen Fixation in Natural and Agricultural Habitats'. T.A. Lie and E.G. Mulder (Eds.). Plant and Soil, Special Vol. pp.495-507.

Pianka, E.R. 1970. On r- and k-selection. Am. Nat. 104: 592-597.

Pitelka, L.F. 1977. Energy allocation in annual and perennial lupines (Lupinus: Leguminosae). Ecology. 58: 1055-1065.

Quarrie, S.A., and H.G. Jones. 1977. Effects of abscisic acid an water stress on development and morphology of wheat. J. Exp. Bot. 28: 192-203.

Ranwell, D.S. 1972. Ecology of salt marshes and sand dunes. Chapman and Hall, London. 258 pp.

Raup, H.M. and G.W. Argus. 1982. The lake Athabasca sand dunes of northern Saskatchewan and Alberta, Canada. I. The land and vegetation. Publ. in Bot. 12: 1-96.

Redmann, R.E. 1976. Plant-water relationship in mixed grassland. Oecol. Berl. 23: 283-295.

Ritchie, G.A., and T. Hinckley. 1975. The pressure chamber as an instrument for ecological research. Advances Ecol. Res. 9: 166-255.

Rowe, J.S. 1972. Forest regions of Canada. Canada Dept. Environment Forest. Serv. Publ. No. 1300. Ottawa, Ont. 172 pp.

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quat. Res. (NY), 3: 444-464.

Rowe, J.S. and R. Hermesh. 1974. Saskatchewan's Athabasca sand dunes. Nature Canada 3: 19-23.

Schaede, R. 1951. Wer die Blaualgensymbiose von Gunnera. Planta 39: 154-170.

Scholander, P.F., H.J. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science N.Y. 148: 339-346.

Schulze, E.D., O.L. Lange, U. Buschbom, L. Kappen, and M. Evenari. 1972. Stomatal responses to changes in humidity in plants growing in the desert. Planta (Berl.) 108: 259-270.

Scotter, G.W. 1964. Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. Can. Wild. Serv. Wild. Management Bull. Ser. 1, 18: 1-111.

Selner, J. and R. Thompson. 1977. Reclamation for afforestation by suitable native and introduced trees and shrubs. AOSERP Report VE.7.1. 93 pp.

Sheriff, D.W. and P.E. Kaye. 1977. Responses of diffusive conductance to humidity in a drought avoiding and a drought resistant legume in terms of stomatal response. Ann. Bot. 41:653-655.

Sheriff, D.W., and H. Meidner. 1974. Water pathways in leaves of Hedera helix L. and Tradescantia virginiana L. J. Exp. Botany 25: 1147-1156.

Shields, L.M. and L.W. Durrell. 1964. Algae in relation to soil fertility. Bot. Review. 30: 92-128.

Skog, J.T. and N.H. Nickerson. 1972. Variation and speciation in the genus Hudsonia. Ann. Missouri Bot. Gard. 59: 454-464.

Slavik, B. 1974. Methods of Studying Plant-Water Relations. Springer-Verlag, New York. 449 pp.

Smith, D.G. 1978. The Athabasca sand dunes. A physical inventory. p. Canada Dept. Indian & North. Aff. Parks Branch, Contract. 104 pp.

Sproule, J.C. 1939. The Pleistocene geology of the Cree Lake region. Saskatchewan Trans. Roy. Soc. Canada, Sect. 4, Ser. 3.33: 101-108.

Stewart, W.D.P. 1967. Transfer of biologically fixed nitrogen in sand dune slack region. Nature 214: 603-604.

Stewart, W.D.P. 1977. Blue-green algae. In, 'A Treatise on Dinitrogen Fixation, Section III: Biology.' R.W.F. Hardy and W.S. Silver (Eds.). John Wiley and Sons, Toronto. pp. 63-125.

Struik, G.J. and J.R. Bray. 1970. Root-shoot ratios of native forest herbs and Zea mays at different soil moisture levels. Ecology 51: 892-893.

Sucoff, E. 1972. Water potential in red pine: Soil moisture, evapotranspiration, crown position. Ecology 53: 681-686.

Sullivan, C.Y., and Eastin, J.D. 1974. Plant physiological responses to water stress. Agric. Meteorol. 14: 113-127.

Taerum, R. 1973. Occurrence of inverted water potential gradients between soil and bean roots. Physiol. Pl. 28: 471-475.

Taylor, H.M., and B. Klepper. 1978. The role of rooting characteristics in the supply of water to plants. Adv. Agron. 30: 99-128.

Thomas, J.C., K.W. Brown, and W.R. Jordan. 1976. Stomatal response to leaf water potential as affected by preconditioning water stress in the field. Agron. J. 68: 706-708.

Thompson, F.B., and L. Layton. 1971. Method for measuring the leaf surface area of complex shoots. Nature 229: 572.

Tremblay, L.P. 1961. Wind striations in northern Alberta and Saskatchewan. Can. Geol. Soc. Bull. 72: 1561-1564.

Turner, N.C. 1974. Mechanisms of regulation of plant growth. Bull. R. Soc. N.Z. 12: 423-432.

Turner, N.C. 1975. Concurrent comparisons of stomatal behavior, water status, and evaporation of maize in soil at high, or low water potential. Pl. Physiol. 55: 932-936.

Turner, N.C. 1977. Drought resistance and adaptation to water-deficits in crop plants. In, 'Stress Physiology In Crop Plants.' H. Mussell and R.C. Staples (Eds.), John Wiley and Sons, New York. pp.344-372.

Turner, N.C., and J.E. Begg. 1978. Response of pasture plants to water deficits. In, 'Plant Relations in Pastures.' J.R. Wilson (Ed.), Melbourne: CSIRO. pp.50-66.

Turner, N.C., and M.J. Long. 1978. Influence of rate of drying and quantum flux densities on the water status and osmotic adjustment of Sorghum. Aust. CSIRO Div. Plant Ind. Ann. Rep. 93.

Tyrell, J.B. and D.B. Dowling. 1897. Report on the country between Athabasca Lake and Churchill River. Canada Dept. Mines, Geol. Surv. Ann. Rept. 1895, N.S. 8. Rept. D.:5-120.

Vaartnou, H. 1976. Revegetation research. AOSERP Report VE.7.2-7.4. 350 pp.

Vieira da Silva, J. 1976. Water stress, ultrastructure and enzymatic activity. In, 'Water and Plant Life: Problems and Modern Approaches.' O.L. Lange, L. Kappen, and E.D. Schulze (Eds.). Springer-Verlag, New York. pp. 207-224.

Vlassak, K., E.A. Paul, and R.E. Harris. 1973. Assessment of biological nitrogen fixation in grassland and associated sites. Plant and Soil 38: 637-649.

Waksman, S.A. 1952. Soil Microbiology. John Wiley and Sons, N.Y. 356 pp.

Weatherley, P.E. 1970. Some aspects of water relations. Adv. Bot. Res. 3: 171-206.

Weinhard, P., J. Balandreau, G. Rinaudo, and Y. Dommerguess. 1971. Non-symbiotic fixation of nitrogen in the rhizosphere of some tropical non-legumes. Rev. Ecol. Biol. Sol. 8:367-373.

Whittaker, R.H. 1962. Net production relations of shrubs in the Great Smoky Mountains. Ecology 43: 357-377.

Wilkinson, A. 1979. Cold hardiness in Ledum groenlandicum. M.Sc. Thesis. Botany Department, University of Alberta. pp.159.

Wilson, A.M., D.N. Hyder, and D.D. Briske. 1976. Drought resitance characteristics of blue grama seedlings. Agron. J. 68: 479-486.

Yoshida, T., and R.R. Ancajas. 1971. Nitrogen fixation by bacteria in the root zone of rice. Soil. Sci. Soc. Am. Proc. 35: 156-158.

Yoshida, T., and R.R. Ancajas. 1973. The fixation of atmospheric nitrogen in the rice rhizosphere. Soil Biol. Biochem. 5: 153-157.